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CAMALLANUS AMERICANUS, nov. spec.,*

A MONOGRAPH ON A NEMATODE SPECIES.

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I. INTRODUCTION

It is as lamentable as interesting that a group of animals presenting so many unusual and important objects of investigation as do the nematodes, should have received so little attention from a general morphological point of view, despite the fact that they have been studied from so many other angles. It is for this reason that systematic studies upon the Nematoda have been so unsatisfactory in the past. With the hope that a very detailed study of the morphology of this group will throw some light on the present chaotic situation, the author has undertaken the study of a single species to find out its precise structure. This work has been done with the hope that it will not only contribute definite information on certain features of anatomy heretofore altogether unknown or at best little described, but will furnish a stimulus to others for investigation along morphological lines in the Nematoda. If as many forms are accurately described among this group as have been in other parasitic classes, there can be no doubt that this difficult branch will be as easily handled systematically as any other.

This work has been done under the direction and with the criticism of Professor Henry Baldwin Ward. To him I express my earnest

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thanks and appreciation. I further wish to thank Dr. Howard B. Lewis and Dr. D. Wright Wilson for suggestions concerning the work on the chemistry of the cuticula, but they assume no responsibility for the results. For material the author is indebted to Dr. Morris M. Wells, the United States Bureau of Fisheries and certain members of the Laboratory of Parasitology at the University of Illinois.

The material used for this study was a parasitic nematode, found usually in the upper two inches of the intestine of certain turtles. This species cannot be identified from any description previously given and is named *Camallanus americanus*, n. sp.

In the table given below it will be seen that this parasite is found in five species belonging to three genera of turtles from different localities as indicated. In addition to these, the same species has been identified from the following hosts in the collection of Professor Ward: *Chrysemys trossti*, *Chrysemys elegans* and *Aromochelys odoratus* from unknown American localities. Seven individuals of *Trionyx spinifer* and two of *Trionyx muticus* examined at Fairport failed to reveal these forms. From these and a few other records it is evident that this parasite occurs from Texas to South Carolina, northward to the great lakes and along the Mississippi river. It seems likely that the parasite is found fairly generally east of the Mississippi river. No information is at hand as regards its distribution west of that stream.

I. TABLE SHOWING EXTENT OF INFECTION

Host species	No. examined	No. infected	No. uninfected	Per Cent infected	Locality
Chelydra serpentina..	4	3	1	75	Fairport, Ia. Urbana, Ill. Raleigh, N. C.
Chrysemys marginata	17	11	6	64	Fairport, Ia. Chicago, Ill.
Chrysemys picta........	6	5	1	83	Raleigh, N. C.
Chrysemys scripta......	8	7	1	87	Raleigh, N. C.
Malacoclemmys lesueuri.................	12	11	1	91	Fairport, Ia.
Total.................	47	37	10	....	

Thus, in the forty-seven turtles examined the percentage of infection averages seventy-eight. In Table I, among the five host species examined, the percentage of infection is lowest in the western painted terrapin. It is interesting to note that in the soft-shelled turtles caught in the same net with the hard-shelled species which were infected, none of these worms were found.

The number of parasites of this species per host ranges from one to several hundred, altho most infected turtles yield about fifteen to twenty. These are found in the intestine just below the stomach with occasionally one or two in the pyloric end of the stomach, or more rarely in the lower region of the gut.

The methods of technique used have been thoroughly discussed in an earlier paper (Magath 1916) and little has been added.

II. GENERAL DESCRIPTION OF PARASITE

These worms are of medium size, rather slender and, when first collected, slightly reddish-brown in color. Perhaps the most noticeable feature is the presence of the golden-brown mouth apparatus, readily seen with the naked eye, and characteristic of the genus. The worms are as a rule moderately active, coiling themselves up into loose knots, but never rolling themselves up spirally, as is the custom of some nematodes, in particular those which are characterized by possessing soft lips.

If a bit of the intestine is placed in a dish with the worms, those coming in contact with it sometimes seize it, and indeed they may be seen to grasp each other in various parts of the body. There is in the anterior region a short clear space, which is occupied by the esophagus, and back of this region is seen the gut, usually dark in outline or even black in some cases, as it appears thru the transparent cuticula. The latter shows fine striations under magnification, and the two sets of three prongs of the oral apparatus can be made out, embedded in the cuticula at the anterior end. Two minute papillae are at the level of the thickest portion of the anterior region of the esophagus; the excretory canal opens about 20 μ anteriad of these papillae.

The posterior region of the males (Fig. 6) is inturned so as to look like the letter "J," the bottom of which presents two medium sized, narrow alae, which are lateral in position; sometimes the longer spiculum is protruded thru the ano-genital aperture.

Nearly all authors have noted the presence of caudal alae on the males within this genus, but the description of the structure is very incomplete. At the anterior margin of the alae, just behind a slight indentation in the body wall on the ventral side, one sees in sections, that the cuticula is split, so that the alae are covered with the outer layer, the body with the inner and a space intervenes. The alae at first arise as a single ventral swelling from the cuticula, but on passing posteriorly they divide and separate more and more from each other, until they come to lie one on either side of the mid-ventral line, and with their ventral margins removed quite a distance from each other. These right and left ala extend to the tip of the tail, remaining about the same size until within a short distance from their terminations, they taper sharply to the tip.

The alae are not very high nor broad (Fig. 87), projecting along their course about 20 μ ventrally and 30 μ laterally beyond the body wall. The outer contour is fairly regular, but here and there is indented or swollen. If the body of the worm be divided in frontal section along the mid-lateral line, it will cut at the level of the dorsal margin of the alae, their ventral margins run parallel to each other, but some distance apart.

Between the two layers of split cuticula there is sometimes present a deeply staining fibrous or granular substance, varying in amount in different individuals. I am unable to state what this substance is, but two possibilities present themselves. The first being that as the cuticula is laid down by the subcuticula underneath this region, it is sloughed off of the lower layer into the alar cavity; the fact that the mass increases with the age of the worms somewhat bears this out. A second theory, suggested to me by Professor Ward, is that this material represents precipitated fluid expressed from the body cavity.

The alae are not without support. Anterior to the anus there are seven pairs of ribs, which are slender and extend at definite intervals between the two split layers of cuticula. Since these supports are discussed elsewhere in the paper, only a few points need be mentioned here. The number and arrangement is like that in *C. seurati*. A rib is like a little slender rod, and anterior to the anus the seven pairs are about equally spaced from each other. In addition to these there are two pairs which are para-anals, very near the anus and on either side; finally there are five pairs situated posteriorly, the anterior

three of either side being grouped together and the last two (Fig. 77). Superficially these last five pairs seem to be pedunculated, with a slight distal enlargement. All of these ribs, unless the postanals are exceptions, are capable of being bent and returning to their original position. They are covered with an exceedingly thin layer of cuticula which is continuous with that of the body wall on the one hand and of the alar wall on the other.

It is interesting to note in passing that Leidy (1851) refers to these structures as "respiratory canals"; he found only six pairs anterior to the anus and did not mention the presence of others posteriorly; whether they were present in *C. trispinosus* is a question. At present one is unable to say whether the number of papillae, ribs or rays is constant for a genus or not; the reports of the number in the different species of the genus Camallanus cannot be looked upon as being reliable.

The females are usually larger than the males, but of about the same ratio so far as the length and thickness of the body are concerned. They are easily recognized from the males by the presence of the large projecting vulva, situated about the middle of the body. The tail is drawn out into a long conical point, without alae, and under a medium magnification shows the presence of three minute spines (Figs. 8,113). Under the same magnification the uterus can be

II. TABLE OF MEASUREMENTS OF ADULT *C. AMERICANUS*

Structure measured	Male	Female
Length	4.9–11.3	7.4–19.4
Greatest width	0.15–0.27	0.16–0.46
Ratio width to length	1:26–1:49	1:33–1:64
Length of postvulva	....	3.2–10.4
Length prevulva	....	4.0–9.2
Ratio postvulva to prevulva	....	1:0.8–1:1.3
Length of tail	....	0.14–0.31
Length of anterior portion of esophagus	0.36–0.44	0.39–0.49
Length of posterior portion of esophagus	0.41–0.70	0.45–0.70
Thickest diameter of esophagus (anterior)	0.086–0.120	0.095–0.131
Length of right spiculum	0.840–0.920	....
Length of left spiculum	0.310	....
Length of caudal alae	0.439–0.793	....

seen to contain motile embryos and some of the coils of the ovary and oviduct can be made out in the anterior end of the body.

Worms kept in water for twenty-four hours or more, are almost transparent as the red color of the body fluid disappears, whereupon the intestine stands out even more clearly.

III. SPECIAL ANATOMY

Cuticula

The cuticular covering of these worms is not unlike that of other nematodes in general appearance. Altho the worms are slightly colored in life, this fact is not due to the presence of coloring matter in the cuticula itself, but rather to a color present in the body fluid, for if worms are cut in two this fluid runs out, leaving the worms without the red color; if kept in water for several days, they get almost colorless, if kept in blood they do not lose their color. The material of which the cuticula is composed is, physically, a highly refractive substance, which may be slightly straw colored. It is elastic and and when stripped off and moist, reminds one of softened gelatin. Reports of pigment in the cuticula of nematodes, especially the parasitic ones, are rare and probably due to misinterpreted facts.

The thickness of the cuticula in these forms varies with the age of the worms to some extent and is thinner in males than females, tho perhaps no thinner in proportion to the length of the worms. The table below gives the average of several measurements made from average adult males and females.

Region measured	Male	Female
Region of jaws	1 μ	3 μ
Anterior third of esophagus	3 μ	4 μ
Middle of body	4 μ	10 μ
Posterior region of body	4 μ	9 μ
Vulva swelling		16 μ
Region of alae	4 μ	
Postanal region	1 μ	1 μ

From this it will be seen that the thickest part of the cuticula is found in the middle of the body and that at either end the cuticula is thinned out. There are slight thickenings of the cuticula extending for a short distance in the anterior region of the body underneath the lateral cephalic ganglia and just outside of the lateral bands.

As in the case of most other nematodes the cuticula of this form is striated (Fig. 29), but the striations are not very pronounced. Striations are seen in embryos which are only 0.542 mm. long. These markings seem to be more conspicuous in the males than in the females and in the latter they are deepest in the posterior region. In the largest individuals these striations are 6 μ apart and half so far apart in females that are no longer than 4.6 mm. It seems probable that as the worms grow the distance of the striations from each other grows so that a worm about 9.0 mm. long will have the same number of striations as the female of half the length; the growth of the cuticula pulls them apart. So far as I could determine these striations do not appear below the outer layer, altho Looss (1905) states that they make an impression upon the subcuticula in *Ancylostoma duodenale.*

In *C. americanus* the cuticula is not made up of a number of complex layers as has been described in the case of the larger Ascaris species. Four layers are found in the largest specimens and each one of these is homogenous. The layers have been named as indicated by the reaction to stains. The thickness of each layer is given as observed in an adult female.

1. Outer dark layer....................	0.3 μ
2. Outer light layer....................	4.0 μ
3. Inner dark layer....................	3.0 μ
4. Inner light layer....................	2.0 μ

No fibrous layer (Fibrillenschicht) nor supporting fibers could be detected within the cuticula, neither could hyaline bodies as described in Ancylostoma be seen. Each layer is homogeneous within itself and the only difference that could be detected between the several layers is their difference in taking stains. The third layer is divided in the middle by a dark line, indicating that it was laid down at two different times, or in two layers, this being also true of the fourth layer (Figs. 26, 27).

In the embryos within the uterus the cuticula is a single homogenous layer and is a little over one micron thick. In a very young female about 5 mm. long the cuticula is only 4 μ thick and shows in its structure only the outer two and a half layers. In a young female, after fecundation but with the embryos mostly in cleavage stages, the cuticula is 6 μ thick in the mid-region of the body,

the outer light layer is formed and is of the same thickness as in the most mature females, the inner dark layer is in the process of being formed and the subcuticula is rather thicker than in the older forms (Fig. 32).

The cuticula is easily stained with any one of the following stains among others: all hematoxylins, orcein, eosin, acid fuschin, gold chloride, thionin (weakly) and orange G. It does not stain with methylene blue or polychromatic methylene blue.

Most authors have used the word "chitin" for this cuticula and the name is also used for the covering and other hard parts of animals in widely separated groups; hence the question has arisen as to the justification of its usage. There seem to be two distinct meanings of the term, one of which is morphological and the other chemical. In morphology the word has been used to cover a great variety of structures for it is applied to coverings of animals, mouth parts, spicula, linings of organs, setae, etc. In chemistry the word has been used to designate a definite chemical compound. Following is given a brief survey of the usage of the word, especially as regards the group of worms, and from this I am inclined to reserve the name for those parts or organs which are chemically chitin, and to use other words for substances which are not of this chemical constitution.

Odier (1832) first used and applied the word chitin to the material composing the covering of certain insects upon which he was working. This early worker not only appreciated its physical but many of its chemical properties, and regarded it as being closely related to the cell coverings found in some plants. He sums up his results in the statement that chitin is a substance which is not dissolved in potash; is soluble in cold sulfuric acid; does not become yellow in nitric acid (negative xanthroproteic test); does not melt on heating and does not contain nitrogen.

More recent investigation has supported this first summary of the properties of the substance, with the exception of the very last statement, there being in the neighborhood of 6% nitrogen in chitin. It is evident that if the term be considered as a morphological one, then only the structures which envelop an organism can be called chitin, while if it is taken in a chemical sense, only those structures which agree with this substance in the coverings of the insects can be called chitin, in short, they must be composed of glucosamine and

acetic acid plus an as yet unidentified nitrogen fraction (Morgulis 1916).

Grube (1850:253) who worked on the cuticular coverings in various forms, stated that among others, Ascaris was covered with a chitinous cuticula; just what he considered to be his evidence is unknown.

It is perhaps due to the authority of Leuckart (1852) that the misunderstanding concerning the name chitin has arisen. This eminent parasitologist maintained that the word "chitin" was a "Collectivbegriff" and stated that the cuticula of Ascaris (Nematoda) and the annelids was composed of chitin. He further included in this list many other forms which do not concern this discussion. Altho he called the substance chitin he knew that it was soluble in alkalis and that chitin of Odier was not, because he gives the properties of the two substances in his paper. Other authors have followed him in his usage of the terms.

Goodrich (1897) recognized a difference in the substance which composed the covering of certain worms and that of the Arthropoda. He states that "so far as the solubilites show, the cuticula appears to be formed of a substance closely allied neither to chitin nor mucin." In addition to this he stated that he obtained a positive xanthroproteic and a modified Millon's test with the cuticula and certain cuticula appendages of these worms.

Sukatschoff (1899) worked on the cuticula of Lumbricus and Ascaris. In the former, in which he was particularly interested he corrected the erroneous statement of Grube, and said that it was not chitin, but conjectured that it belonged within a group of proteins known as albuminoids.

Finally Reichart (1902) proposed the name *cornein*, a name first used by Valenciennes (1855), for the substance which covers the bodies of annelids, or most of them and Ascaris, basing his claim on the quantitative chemical analysis in the case of annelids and corresponding qualitative tests of both forms. With this last investigator I can agree and present here the results of my investigations. The form used was *Ascaris suum* from the hog, since the same qualitative tests hold good for *C. americanus* and other nematodes, the chemical composition of the cuticula is essentially the same in the entire group of nematodes.

The material was obtained fresh, and prepared by scraping the cuticula free from the underlying tissue and then washing it thoroly in distilled water, after which it was dried to a constant weight in an oven at 70° C. Cuticula prepared in this way gives the following results in chemical analysis:

It is insoluble in cold water, but goes partly into solution in boiling water, swelling to some extent in either. It is insoluble in alcohol, ether, chloroform, or acetic acid, but swells in the last reagent. It is further insoluble in dilute mineral acids, but will dissolve upon standing in either concentrated sulfuric or nitric acid. It is soluble in hot concentrated acids and in cold caustic alkalis, even when only 1% concentrated upon standing and readily when heated to 70° C. It is soluble in ammonium hydroxid.

According to Burge and Burge (1915) and Reichard (1902) the cuticula of Ascaris is digested by the action of enzymes; I have not repeated these experiments but can see no reason for doubting them.

Tests for the presence of uric acid, creatin and urea have been negative, as have also been the repeated attempts to obtain a reduction with Fehling's solution, either before or after hydrolysis.

With Millon's reagent the test does not result in a very strong red color and sometimes seen to be totally negative. Xanthroproteic and Hopkin-Cole tests are positive. With the biuret test a deep purple color develops like that resulting in the presence of peptones and gelatin. The test for unoxidized sulfur was positive. On hydrolysis no tryosin could be detected.

The total amount of sulfur was determined in two samples with the following results:

I. 0.2318 gm.	1.25% sulfur
II. 0.2384 gm.	1.16% sulfur
Average	1.20% sulfur

Total nitrogen was determined by the Kjeldahl method and the two samples yielded:

I. 0.2020 gm.	16.90% nitrogen
II. 0.2113 gm.	17.04% nitrogen
Average	16.97% nitrogen

A small amount of cuticula was boiled in water for several hours and the solution filtered. After the filtrate was precipitated with

alcohol and filtered, the dried precipitate was tested for free and combined tryptophane. No free acid was found but the Hopkins-Cole test was still positive. A test for cystine was also positive in the filtrate.

From the foregoing observations it is at once evident that the substance of which the cuticula is composed is not chitin but an albuminoid. On closer observation it becomes obvious that chemically it more nearly resembles the group of albuminoids represented by collagen, elastin and gelatin than any others in the group. In all these the total nitrogen is high, ranging around 17 % and the sulfur is usually above 0.5 % (of course is pure gelatin there is no cystine and hence no sulfur) altho in my particular samples the sulfur is a little high. If the total nitrogen analysis is compared with those offered for cornein in other animals, it will be seen that they all are very near alike, thus the list below demonstrates.

16.8 %	Fremy
17.06%	Krukenberg
16.76%	Krukenberg
16.60%	Krukenberg
16.97%	Magath

In addition to this the qualitative properties are the same in all these cases. If one looks a little more closely into the relation of cornein with gelatin, collogen, etc., he will at once be struck by the fact that with formol all are hardened and rendered insoluble. This is the basis for the statement (Magath 1916) that formol in useless as a killing and fixing agent for nematodes, except in one special technique. The result with the biuret reaction is again significant, the absence of tyrosin, the swelling phenomenon with acetic acid and water, and the general physical appearance relate it very definitely to this series of proteins.

The fact that the cuticula is digested by the action of enzymes, is relatively low in sulfur and high in nitrogen excludes it from the keratin series, which is characterized by the opposite properties; the fact that it has no sugar in combination with it excludes a close relationship with the mucoids. To compare this substance with chitin one should recall, the low percentage of nitrogen present in chitin, its insolubility in caustic alkalis, its resistance to the action of

enzymes and its glucose molecule; these facts make it impossible to call the cuticula of nematodes chitin.

Attention should be called to a paper by Flury (1912) who presents some work on the chemistry of the cuticula of Ascaris. The results agree very closely with these presented here with the exception of the determination of sulfur. Flury found 4.3 % in his samples which is much higher than I have found. He concludes that the substance is keratin, but objections to this conclusion have already been pointed out.

In conclusion then, the cuticula of nematodes, and as previous authors have pointed out the cuticula of most of the worms, is composed of cornein, an albuminoid closely related to the albuminoids of connective and supportive tissue and is a differentiation product and not a solidified secretion (Leydig, 1888, and Rauther, 1905).

Subcuticula and Longitudinal Lines

A. Female

In general, the subcuticula of this species is not unlike in arrangement that of *Ancylostoma duodenale* as described by Looss.

No nuclei can be found in the very thin layer between the muscle cells and the cuticula. In the oldest worms no subcuticula layer can be demonstrated at all except in the thickened areas known as the longitudinal lines. In some cases the muscles seem to be applied directly to the inner margin of the cuticula. In the younger individuals there can be occasionally seen a few strands of tissue, continuous with the longitudinal lines, and because it lies underneath the cuticula it has been interpreted as being the subcuticula, but at best this layer is very poorly developed in *C. americanus*. Because no nuclei appear in this tissue it should be considered as being a syncytium which embraces the longitudinal lines and certain other parts to be mentioned in other sections of the paper.

The anterior origin of the four longitudinal lines, there are no subdorsals or subventrals in this species, is very interesting and at the same time extremely difficult to work out. Unexplained structures have been noted by previous authors in the "head" region of nematodes and even in Mermis, Rauther (1906) has described them briefly, but as will be shown, correctly attributes them to special modifications on the longitudinal lines.

Looss (1901, 1905) referred to structures, which from his text and figures, I consider to be homologous structures in the Sclerostomidae and *A. duodenale.* He named these structures the "ligamentum cephalo-oesophageale" stating that this was a structure "sui generis" and while he admits (1905:53) that the lateral lines rise slightly in height in this region and offer support for the cells of the "ligament," he mentions no dorsal and ventral connections with the subcuticula, nor does he make it clear that he considers this structure of subcuticula origin. His idea of the function of the structure is set forth in the following statement: (1905:77) "it is intended to attach and to secure the chitinous mouth capsule to the muscular oesophagus." Looss (1901) suggested for this structure a function in the motion of these parts, thus indicating a muscular connection.

The description which Looss gives of these structures in *A. duodenale* is not very complete, since he himself admits the difficulty of working out the region on account of the sections breaking out, due to the hard parts of the mouth capsule, but I am inclined to believe from the description given, that in the following parts of *C. americanus* I am dealing with homologous structures and not greatly unlike those in *A. duodenale.*

Figure 14 shows four pairs of loose granular masses lying in the angles formed by the lateral plates of the jaws and the tridents. Passing posteriorly the two members of each pair unite; each pair is therefore formed by the division of a single structure. This union takes place just below the anterior margin of the oesophagus. The anterior ends of these pairs of protoplasmic masses are seen just posterior to the anterior margins of the jaws. In a series of sections passing anteroposteriorly, the lateral lines appear just behind the anterior insertions of the four giant jaw muscles as narrow bands dividing each right and left pairs. They soon send out tissue which applies itself around the outer margins of the lateral plates and soon joins with the median member of each pair of granular areas. A single large nucleus appears in each lateral line anterior to the beginning of the oesophagus. The lateral lines increase in size as one passes posteriorly until at the level of the beginning of the oesophagus they branch out, tissue from them serving to fill in the space between the esophagus, body walls and the muscle cells. Here three more nuclei

appear in each lateral line. The tissue of the lateral lines is continuous with the end of the esophagus in the young forms, but in older animals this tissue has formed the esophageal cap and still retains its connection with that structure. The cap it not smooth but looks as though it had a scolloped border.

Fifteen micra below this level the dorsal and ventral lines make their appearances and then in the region from here to the nerve ring, the esophagus is surrounded by subcuticula tissue which originates from the longitudinal lines and forms a commissure around the oesophagus. The mass of tissue is syncytial, but presents very difinite structures or thickenings around very large spherical nuclei; the rest of the tissue is chiefly fibrous. Of these thickenings there are five dorsal and an equal number in the ventral field, the two most lateral of each represents the united granular masses which extend anteriorly, the middle one of each five being the inner end of the dorsal and ventral lines. Each thickening has two large nuclei, all twenty nuclei being contained within a distance of 50 μ. Here and there, scattered thruout this region, are nerve cells which will be considered in another section. In the middle of this region appear two more nuclei in each lateral line, making six in each before they divide into dorsal and ventral halves.

Near the end of this region under discussion appear two ovoid nuclei in the dorsal line, there are two more spherical ones in the ventral but further separated from each other. In the region of the nerve ring the lines present broadened surfaces towards it. In addition to these nuclei in the dorsal and ventral lines are two others in each, small and just at the anterior margins of these lines.

This tissue seems to me to represent nothing more nor less than the anterior origin of the subcuticula. It acts in this region as support, primarily perhaps, for the nervous tissue, but undoubtedly forms in some manner the esophageal cap and in all probability it contributes to the mouth parts, which are cuticula products and should be formed from the same type of tissue as the body covering; here is where the two structures make intimate contact with each other. It is impossible to consider this as a ligament for mouth apparatus and esophageal connection in *C. americanus* for here the chief parts of the structure lie too far posteriorly and from Looss' description this must be true in Ancylostoma as well. Furthermore

there are similar structures in species without hard oral parts and these interesting thickenings of subcuticula certainly occur in Mermis.

Roughly speaking the subcuticula fills up the region between the esophagus and the body wall, the nerve ring and base of the oral apparatus; this is the tissue seen within this region as so complicated a structure.

Interesting in this connection is the fact that the position of the nuclei and number in the various parts of this region have been found to be constant in all the specimens examined, perhaps as many as ten in all, but the fewness and apparent individuality of these nuclei offer no surprising revelations in the field of "cell constancy" (Figs. 34, 35, 46-49).

The thickening of the subcuticula forming the dorsal line is by far the smallest and most inconspicuous of all the longitudinal lines, but extends nearly the entire length of the body. It begins anterior to the nerve ring and extends to the posterior tip of the tail. Thruout the middle region of the body it becomes so insignificant as to be entirely overlooked, but posteriorly it increases rather suddenly and remains rather thick until within a few micra of the posterior tip. There are in this structure a few nuclei, and below the anus there are three, equally spaced and rather large. The muscles in the dorsal half of the body send more projections to this band than those in the anterior half.

The ventral line is much more conspicuous than the dorsal one, but like it diminishes greatly in size thruout the mid region of the body. Anteriorly it begins about at the level of the beginning of the dorsal line and has quite the same fate in the posterior part, with the exception of becoming involved with other structures which will be taken up separately. About the level of the posterior fifth of the body the ventral line enlarges greatly and is like a flat cushion extending along the mid-ventral line. In the region of the anus it becomes very wide and is even more conspicuous post-anally. There are three nuclei in this region, equally spaced to correspond to the three in the dorsal line (Fig. 116). Preanally there are nuclei in the ventral line, but they are very small and far apart. The regions of the lines posterior to the anus have been called the "pulvillus postanalis" in *A. duodenale* by Looss, but little justification can be found for the

continued use of the term, for this region is merely the posterior part of the dorsal line and deserves no particular name. Special modifications of this structure will be discussed elsewhere as for example in the sections on the vulva, rectum, etc.

As in *A. duodenale,* the lateral lines (Figs. 46, 50, 57, 117) of this species arise in the anterior region of the body as a thickened region of the subcuticula which is undivided at first. Looss says that these lines arise shortly behind the anterior margin of the oral apparatus in *A. duodenale* which is also true of *C. americanus.* As a matter of fact they seem to begin just posterior to the region of the anterior insertion of the four giant muscle cells of the jaws; below their posterior insertions they are narrow but project well out into the body cavity. Shortly behind their origin the divisional septum is seen and from thence posteriorly they are divided into dorsal and ventral halves. Two regions are fairly well marked out in the lateral lines. Around the outer membrane which covers them on the interior side, the protoplasm is very dense and granular, in this region and lying towards the mesiad, there appears as Looss suggested, a tissue of "softer" material and "watery." Often in older specimens this area is totally devoid of stainable material and when there is material present it is not unlike that which precipitates in the body cavity. Around the "partition wall" the protoplasm is thickened; no nuclei appear either in this region or in the inner area. In the part of the lateral lines applied to the inner margins of the cuticula one recognizes the second region. In here are found nuclei, rather large and frequent in distribution, especially in the posterior region of the body. The tissue is decidedly of the nature of a syncytium and very fibrous in character, the Stützfibrillen originate here, and in larger species have been traced out into the subcuticula and into the muscle cells; in this form the structures are too minute to be demonstrated if they exist. Occassionally a nucleus is seen at the outer base of the "partition wall" and these nuclei are believed to belong to the structure K. C. Schneider (1902) speaks of as a row of cells, "mediale Zellreihe," in Ascaris, being homologous in these species.

During the course thruout the length of the body, no special details of the lateral lines need mention; in older females they become compressed as the uterus fills with embryos, but here and there extend out into the body cavity when not interferred with by other organs.

Near the posterior tip of the tail the lines occupy a large percentage of the entire circumference of the body and have less "watery" material within them. They disappear in the subcuticula of the tip of the tail. In young forms the lateral lines occupy a large percentage of the body cavity (Fig. 124).

B. Males

The conditions described for the females as regards the subcuticula and longitudinal lines are almost duplicated in the males, but with some slight modifications, chief of which are due to the apparent displacement of the lateral lines in the posterior region of the body. These are located so that they appear to lie on the dorsal wall, but in reality this is not the case. The enormous development of the muscles of the male tail takes place entirely below the lateral lines, i.e., in the ventral half of the body, which causes them to appear far dorsal, so that they no longer divide the body into approximately equal halves. The arrangement of the parts of the subcuticula in the posterior region of the body below the anus is like that in the females.

The Excretory System

Altho Bojanus and Cloquet (1824) noted the presence of canals in the lateral lines of nematodes, it remained for von Siebold (1838) to attach a significance to these organs, and it was he who first noted that they were connected with a duct which opened on the surface of the body. He however admitted the puzzling nature of their function: "Zu welchen Zwecke das in diesen Organen abgesonderte homogene und farblose Sekret dienen soll, wurde noch nicht ermittelt." Subsequent authors up to the time of Schneider (1866) added nothing of value to the observations of von Siebold and even Schneider was able to make only a few guesses as to the true nature of these organs. About this time the work of Bastian (1866) appeared in which he stated that the whole structure came from a single cell and compared the organs to the so-called "water-vascular system" in trematodes. Leuckart added nothing of value to the statements of Schneider, but upon his authority nearly all workers since have looked for the excretory function of the nematodes in the lateral lines and the canals anatomically connected with them.

Stimulated by the observations of Kovalesky followed by Metalnikow (1897), Nassanow (1897 to 1900a) investigated this interesting system by means of injecting certain substances into the body cavity and observing the results. The second of these authors mentioned obtained chiefly negative results; in only two instances did he observe the massing of the stains; he used suspensions of carmin, etc., within the lateral lines. However, he noted the appearance of certain stains in the cells of the middle intestine and was forced to the conclusion that while the lateral lines may play some part in the excretory function, the gut itself must be quite a factor in the elimination of certain materials from the body. Nassanow repeated the experiments and also noted the action of the midgut, but was able to detect the presence of frog's blood, when injected into the body cavity, within the canals themselves, and so attached some importance to these structures. He, it was, who investigated the phagocytic organs, and came to the conclusion that they are like lymph glands, giving rise to ameboid cells which pass through the body cavity, collecting foreign materials and destroying it. He is not very clear as to the final elimination of the destroyed materials, but one may surmise that this also passes through the lateral canals or gut wall.

Golowin (1902) carried on a very extensive investigation of the problem and his results, so far as the excretory system proper is concerned, may be summarized as follows:

1. Most of the stains used by the former investigators are precipitated in the body cavity, and hence their negative results are explained. They must be in solution before they can get into the lateral canals.

2. When colored solutions are injected they may be watched as they pass into the lateral lines, canals, and finally out thru the excretory pore, and the amount of excretion can be determined quantitativly by means of the colorimeter.

3. Staining of the lateral lines in the few cases in which it was noted in the use of suspensions, is explained by the fact that the animals died first, this is true as well in the case of the staining of the phagocytic organs, midgut, etc.

4. The lateral lines are engaged in the excretory process as well as the canals.

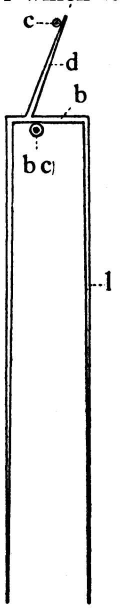
Looss (1905) after investigating the cervical glands in Ancylostoma came to the conclusion that they represent "integral component parts of the excretory apparatus," and not glands, but he wisely reserved his final decision of the whole matter until further investigation of the system has been made.

One year later Goldschmidt, (1906) in his characteristic dogmatic way, gave his conception of the system. It arises from a single cell, a radiating nucleus lies in the left leg posterior to the arcadelike portion. The canal is lost in a circle of nuclei in a smaller canal, which itself then narrows before a nucleus. The two lateral canals, lying in the lateral lines, connect in the anterior part of the body thru an arcade, called a "bridge." There is in Ascaris some complications of the canals in the anterior region, of no importance here, but finally an exit is made by means of a single ventral pore. Posteriorly the lateral canals end blindly. The lining of the canals is difficult to describe, but looks something like glass. There is around this inner lining a plasmatic substance, but neither of these structures suggests in the least the excreting cells of other forms. The tissue on either side of the canals in each line is glandular in nature, and Goldschmidt thought that he had recognized an excretion from them into the canals themselves, thru small pores. The lateral lines in part then, are excretory in function and the syncytium around them is a passage way for materials going into the canals.

The research of Rauther (1907) is very interesting in a comparative way. He concerned himself with the free-living nematodes and after working with indigo carmin, found that whether it was taken in by the mouth, e.g., with food, or thru the skin, that the excretion was indirect. It was finally excreted thru the gut, which he compared to a urinary duct, and the esophagus, which he compared to the Malpighian capsules. He eliminated the glands of the esophagus as functioning in the process and found that the process was carried on by the muscles of the organ. The chemicals were absorbed and eliminated by the gut. He suggested that the pigment masses in the intestines of certain parasitic forms were stages in the excretion process.

If Goldschmidt and Rauther are both correct it is interesting to note that there is a marked difference in the method of elimination of excretory products between the free-living and perasitic nematodes

and such forms in the parasitic groups as do have no lateral lines and canals, or only poorly developed ones, present interesting cases. It occurred to the author that there must be forms present in which the function is divided between the alimentary canal and the lateral lines, but may function or there may remain some indication of function in either case. The species used in this work at once suggested a possibility, from the anatomical relations of its parts. In the first place there is a divided esophagus, the most posterior portion of which it histologically quite different from the anterior portion. In the next place the bridge is in the region of the lower part. Finally this portion is covered with *an out-growth from the tissue of the lateral lines.*



Textfigue A. Diagram showing the general arrangement of the excretory system. *b.* excretory bridge; *b. c.* excretory bridge cell; *c.* carrying cell of excretory duct; *d.* excretory duct; *l.* lateral excretory canal.

In *C. americanus* the canals themselves lie in the lateral lines, in a V-shaped area formed by the union of the dorsal and ventral halves, which is turned towards the body cavity. Here there is a thickened portion and very granular, but devoid of nuclei (Fig. 57). These canals are in the lateral lines since their inner boundry is always seen between the canals and the body cavity, except where they leave to form the bridge, to be spoken of later. The canals begin in the posterior third of the body as blind tubes and pass forward to about the level of the anterior fifth of the posterior part of the esophagus, where they each bend towards the ventral line, anastomosing with each other; then there passes, anteriorly and slightly to the left of the median line, a small duct, which after making a sharp turn outwards and mediad, opens about 0.35 mm. from the anterior tip of the body and between the later cervical papillae and the nerve ring (Fig. 50, also Textfig. A).

The histological details of this system in nematodes have been discussed by the previous workers of whom K. C. Schneider gives a correct account of the condition in Ascaris; that in *C. americanus* is not greatly different except in certain features. It seems well to consider the canals being composed of two

layers, the inner of which is highly refractive and of a substance recalling the cuticula from which it is believed by most authors to have been derived; it must be stated that it stains differently and does not seem to be continuous with the cuticula in the adults. To this statement must be added that the mechanics of getting this long bifid tube lined by the invasion of cuticula thru a very minute pore at one end is not at all easy to explain, and the suggestion that it is lined with a transformation product from the outer layer of its own wall is not an unreasonable one; in the absence of absolute embryological evidence for either position the latter seems as plausable as the first suggestion. The outer layer (*sarc*) is almost as monotonous as the inner. This layer is granular in nature, stains with the cytoplasmic stains much more intensely than the lateral lines, and often has in it rather deeply staining granules, which stand out sharply. These are nearer the periphery of the wall than the lumen, which is about one to two micra in diameter.

Perhaps the granules have been mistaken by some authors for nuclei and would account for the statement made by Shipley (1910) that there are nuclei in this layer. One is unable to find the best authors considering this as a nucleated layer and it has been shown that the whole structure proceeds from a single anterior cell.

As the ducts pass anteriorly they enlarge, especially does the wall get thicker, while the lumen enlarges but slightly. At a level with the anterior margin of the intestine the entire duct is, in the females, about 8 μ in diameter, while just poserior to the bridge it is 10 μ.

At a position which varies within a distance of the level of the anterior fifth of the posterior region of the esophagus, the right and left canals bend towards the mid-ventral line and here lie in a thickened portion of the wall of the ducts, in a substance known as the "bridge" (Figs. 3, 51, 56). Lying to the left of the mid-line is a single large nucleus, oval or nearly round in shape, and 15 μ in diameter, containing a nucleolus 5 μ in diameter. The tissue of the bridge is continuous with the outer layer of the canals and of the same histological properties, within it can be seen the minute lumen of the duct and the inner layer of refractive material. On the ventral side of the esophagus where the bridge lies, the two are in close contact

with each other. The only wall existing between them is that of the tunica propria of the esophagus, and in some specimens even this cannot be detected. In either event the bridge partially encloses the esophagus on the ventral side. Furthermore, there is enveloping the whole of the posterior region of the esophagus a tissue (Figs. 31, 33) not unlike the outer layer of the canals and which seems to be made of a tissue from them and partly from the inner margins of the lateral lines. A small nucleus can be seen in this tissue between the left side of the esophagus and the inner portion of the lateral lines below the bridge.

Where the duct turns to open to the exterior, there is a nucleus (Fig. 50) which is located just on top of the duct and medial to it. This is considered the nucleus of the carrying cell of the excretory vesicle and this cell envelops the canal in this region. It probably functions as a supporting cell as well, since no other cell is present.

The rather suggestive histology of the posterior portion of the esophagus and the lack of excreting tissue with nuclei in the lateral lines as in the case of Ascaris, together with the fact that the bridge and the accessory tissue are so closely associated with the esophagus has led to a conclusion, which if true, has some bearing on conceptions of the excretory function of these forms.

The bridge is so closely associated with the esophagus that the latter stands in the same relation to the lumen of the canals as do the lateral lines, and I believe from the nature of the structure of this portion of the esophagus, that it has to do with the excretory function, that the excretory products instead of passing thru the lumen of the gut as Rauther found in the case of the free-living nematodes, passes thru the tissue of the esophagus and then into the lateral ducts in whatever fashion this could take place in the lateral bands, whether thru minute pores or by absorption, in which event hydrophylic proteins or their derivitives should be looked for as agents. Under the last condition the thin lining will have to be permeable, which would increase the possibility of this system being excretory.

If one allow that the posterior portion of the esophagus can and does act as the excretory apparatus in part or in the whole, these forms will be intermediate between the free-living and the more highly developed parasitic nematodes, so far as this function is concerned.

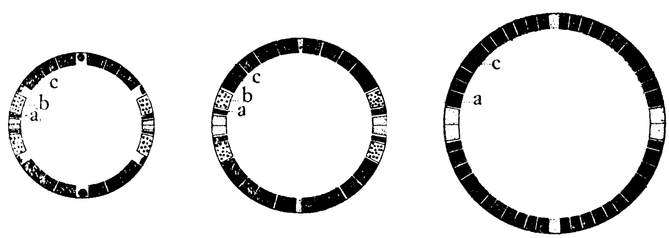
It is rather interesting to note in this connection that most of the nematode parasites so far recorded from water hosts are characterized by the possession of two or more regions of the esophagus, ceca, etc.; forms which are found in both water and land hosts have, to a great extent, an esophageal bulb, with this group are numberous nematode parasites of insects which live in moist decaying material, and some hosts which spend part of their lives in the water; the strictly land parasites have usually a simple esophagus. It is not unreasonable to suppose that the first forms to become parasitized would be the water hosts, since the free living nematodes are mostly found in water or mud. If this be true one would expect the nematodes of these hosts to be closer related to the free-living forms than those of the land hosts. It is an interesting speculation and one with some foundation, to suppose that these forms found in the water hosts represent forms that stand below the bulbed esophageal species, e.g., the Heterakidae, which in turn are below the forms with the type of the esophagus found in Ascaris, so far as parasitism is concerned. These more primative nematodes have retained in part, if not entirely, the function of excretion within the esophagus and are in this respect but slightly more advanced than the free-living species. Interesting are the various members of the Superfamily Spiruroidea, in which one can find varying degrees of esophageal division, some of which have been pointed out by Ward and Magath (1917).

Finally in this connection should be mentioned the rather peculiar group of Trichosyringata, in which the esophagus is not muscular but composed of a capillary tube, passing thru a row of cells. These forms have very small lateral lines and Rauther (1906) has maintained that in Mermis, a form he has studied, that the "spindelförmigen Zellen des hintern Oesophagus" are the "Excretionzellen" of this form and are homologous to the ventral bridge cell in Ascaris. *Camallanus americanus* then would lie between the two great groups proposed by Ward. Stephens (1916) suggests an excretory function for certain "skin glands" found in some nematodes in the group of Trichosyringata, but Rauther's suggestion seems better founded both on fact and theory.

Somatic Musculature

The somatic muscles begin anteriorly on a level with the ring of the mouth apparatus. Here they first appear on the dorsal and

ventral sides of the body, closely applied to the cuticula and between the fields marked out by the tridents. The lateral fields are still occupied by the four giant muscle cells which open the jaws. Three cells between each median and lateral branch of the tridents come into existence at once, so there are three cells in each quadrant, the one nearest the lateral margin being nearly twice as large as either of the other two. A few micra posteriorly three other muscles enter each field, the large cell in each case being pushed laterally, so that the last cells enter between them and the mid-dorsal or ventral line, as the case may be. Other cells enter shortly and the giant cells in the lateral lines are quickly undermined by the fibrillar portions of the general body muscle cells, which are large cells of the same size as those previously mentioned. At the level of the nerve ring there are, if one quadrant is considered, six cells between the first large cell and the mid-dorsal or ventral line; this cell makes the seventh, and between it and the mid-lateral line there are two more, of which the most lateral is a large one. Finally there enters another small one between the last and the lateral margin, thus making ten cells in each quadrant. This last muscle cell can be traced to the level of the anterior margin of the esophagus, where it appears in each quadrant and as a single fibrillar element. It remains thus until at the level of the nerve ring it increases in size, takes on the characteristic shape of the general body muscle cells, and possesses a sarcoplasmic portion when the similar portion of the giant cells disappears below the level of the nerve ring. The series of diagrams shows how these muscle cells originate (Textfig. B).



Textfigure B. Schematic representation of the anterior origin of the somatic muscle cells *a*, is the same muscle cell in each figure; *b*, is the giant muscle cells of the valves; *c*, is the same cell in each figure. The lateral lines are indicated as are also the dorsal and ventral ones, by fine stipling.

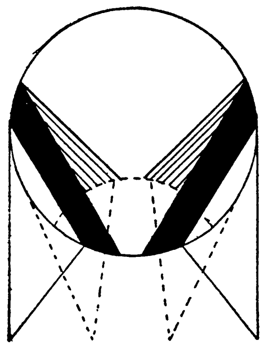
On passing posteriorly the differences in the sizes of the various cells is lost, so that below the level of the posterior margin of the esophagus they seem to be of uniform size. Processes bend over to the dorsal and ventral nerves, none were seen going to the lateral lines, so that a cross section gives the impression that they lean from the sides towards the mid-lines (Figs. 55, 123). In the posterior region this tendency is even more marked, where the processes can be seen very clearly and to come into contact with the nerve, especially the ventral nerve. As the cells are anteriorly of about the same height, the appearance is that of an even circle when seen in cross section, formed by the tops of the cells (Fig. 51).

Posteriorly the number of cells diminishes, first in the ventral fields, so that there are but two in the ventral quadrants and four in the dorsal ones, at the level of the anus. Posterior to the anus they are diminished further, until in the tip there are finally but four muscle cells, one in each quadrant.

In the males the somatic muscles in the caudal end are evidently modified to be useful in the act of copulation (Figs. 87, 92).

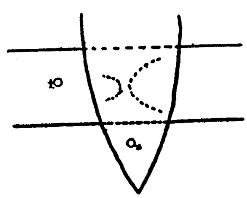
Beginning about the level of the lateral alae the fibrillar portions of two regions of the somatic muscles elongate towards the body cavity. The two regions are found just ventral to the lateral lines on the one hand, and on the other hand just lateral on either side of the ventral line. At first only one or two muscle cells are involved and so a corresponding cell from each region on the same side comes to have its fibrillar portion connected and thus there extends a muscle from a ventral-lateral to a lateral-ventral position, a cross section of the body presenting the appearance of oblique muscles on either side of the ventral field. More cells become involved as one passes posteriorly so that there are about as many bridging the gap as are left between the two places of insertion. This means that there are more than a fourth of all the muscles of the caudal end of the body involved, since the lateral lines have already been pushed far dorsally. The nuclei of these cells are surrounded by a small amount of protoplasm, in the center of the cell. This condition continues even a short distance below the anus, then the regular somatic muscles continue and end in the same manner as in the case of the female.

Action of the muscles in the caudal end of the males. The diagram (Textfig. C) shows the mode of action of these muscles. Their con-



Textfigure C. Diagram illustrating the action of the caudal muscles of the male. The dotted lines indicate the position of the alae when the muscles have contracted pulling up the ventrum of the body. By this method the male grasps the vulva of the female.

traction raises the ventral side of the body. Normally the lateral alae stand out from the body of the male leaving quite a little space between the right and left alae, but when these caudal muscles contract they pull the ventral side of the body up thus serving to bring together the two lateral alae. These muscles are antagonized by the elasticity of the body cuticula, and when they relax the lateral alae are again allowed to swing outward. The usefulness of this arrangement is clearly seen in the act of copulation. Here the male comes to lie at right angles to the female and with the alae stradling the vulva (Textfig. D). Then the caudal muscles contract and this pulls



Textfigure D. Diagram showing the position of the male and female during copulation.

in and down the alae, thus forming a firm hold over the two lips of the vulva, which are suited by their structure to just this sort of action. The connection is made not by the use of suction nor by the

use of cement, but rather by the mere mechanical grip of the two wings. Of course the insertion of the spicula—either one or two, for I cannot say whether the smaller one functions—helps to hold the two worms together.

Here the methods of copulation as known in the Nematoda may be briefly reviewed.

(1) The action of cement and a bursa. An example is found in Ancylostoma, where the bursa opens and closes by the action of special muscles and also furnishes a broad surface for the application of cement, which is the chief means of holding the male against the female.

(2) The use of a sucker. An example is Heterakis in which a large sucker exists in the male and is used to attach it to the female. The action of this sucker, according to Schneider, is effected by a series of muscles radiating from the bottom of the organ to the edges of the lateral lines. Their contraction creates a small vacuum which is released after copulation by the action of the fluid of the body.

(3) The case given in this paper, where a mechanical grip serves to make the male fast to the female.

There are undoubtedly other means of copulation in the nematodes, but no others are sufficiently well-known to be given here. These three methods are dependent upon certain distinct morphological differences in the anatomy of the forms in question and presents an interesting field for research which may lead to a good means of classification. The vulva of the females will also need to be studied for it may furnish a clue, because it is modified according to the *modus operandi* of the males.

Histology of the somatic muscle cells. These cells are, like the muscle cells of other nematodes, composed of two portions, the fibrillar and sarcoplasmic. In the cells of the anterior region of the body, anterior to the posterior margin of the esophagus, the latter portion is larger than the former, while in the rest of the body they are of about equal size. The fibrilla part is in the shape of a V or U, with the notch varying in depth from a barely perceptible one, until in some cells, it appears to cut in half the depth of the outer layer. In the fibrillar layer the muscle bands (Muskelleisten) are placed very closely together so that it is not possible to count the number accurately, altho they are estimated as being nearly one hundred in each

cell (Figs. 25, 28). Supporting fibers (Stützfibrille) cannot be seen in this layer. The muscle bands are arranged along three faces of the cell, on the face nearest the cuticula and on the two vertical sides, so that the bands come together in a sharp angle in two diagonal lines. A little thickening of the protoplasm occurs around the margins of the cells. The sarcoplasmic parts of the cells stick out into the general body cavity, somewhat beyond the inner margins of the fibrillar layer. In this portion one can see a very large nucleus, oval in shape and 6 μ long, containing but one nucleolus, which is rather large and stains deeply with hematoxylin stains. Around the nucleus is a dark staining area, the "Gitterkörbchen" of Bilek (1909), which he has shown to be made up of the supporting fibers of the cells, and from this area, in well preserved specimens can be seen very minute fibrills, which can be traced out thru the sarcoplasmic part of the cell. They probably pass into the contractile layer and thence into the subcuticula as Bilek (1910) has shown in the case of *A. lumbricoides* and *megalocephala*. The sarcoplasm consists of fine granular material, which stains a light red with van Gieson's stain and blue with Mallory's and Delafield's hematoxylin.

The fibrillar portion stains with picric acid and the anilin stains, or with chrom-hematoxylin. The bands stain but slightly darker than the ground substance of the fibrillar layer.

The anterior cells are perhaps no longer than 0.2 mm. while posteriorly the cells are as long as 1 mm. in some cases. A typical anterior cell is compared with a typical posterior one in the following table:

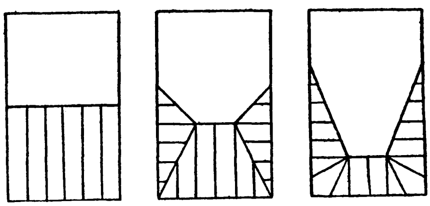
Place of measurement	Anterior cell	Posterior cell
Width	0.013 mm.	0.013 mm.
Thickness	0.020 mm.	0.015 mm.
Thickest part of sarcoplasma	0.016 mm.	0.008 mm.

The muscle cells of this form are very much like those of *Ancylostoma duodenale* as described by Looss (1905) both as regards size and structure. It is interesting to note that while this is true, there are in the hookworm only eight cells around the body as seen in cross section, while there are about forty in the new species. As in the case of *A. duodenale* there may be several sarcoplasmic processes from

each cell, and these also anastomose with each other, and seem in some cases to come into contact with the internal organs.

As compared with the muscle cells of *Oxyuris curvula* (Ehlers 1899) they are quite different. Here the cells are 8.69 mm. long and 0.51 mm. wide. There is next to the subcuticula a flat layer of contractile material, then placed on this is a granular unstainable portion, and finally an intensively staining rind layer. Each muscle cell has a nucleus.

The type of muscle cell in the larger members of the genus Ascaris is so well known that it needs little attention here. The contractile portion is in the shape of a very deep U with the sarcoplasmic portion extending out from it and containing a large nucleus with its accumulation of supporting fibers around it. These fibers pass into the ground substance of the contractile part and finally into the subcuticula. The sarcoplasmic layer is in contact with the fibrillar layer nearly all the way down to the bottom of the U, which is very near the subcuticula layer. The diagram illustrates the three conditions mentioned above (Textfig. E).



Oxyuris Cammallanus Ascaris

Textfigure E. Diagram illustrating the relative amount of Sarcoplasmic and Fibrillar portions of muscle cells in different nematode genera.

Schneider (1860) proposed two names to be applied to divisions of the Class Nematoda, based on the structure of the muscle cells. The name "Platymyarier" was applied to all nematodes in which the fibrillar portion of the muscle was flat towards the body cavity, typically in the case of Oxyuris. The "Coelomyarier" include the nematodes in which the fibrillar portion was notched so that the sarcoplasmic part dipped down into and between the contractile layer, which was present on either side of the cell and on the outer margin.

Further Schneider recognized a difference in the muscular system of Gordius and Mermis and he (1886) proposed the name Holo-

myarii to include these forms along with certain other Nematoda. However, Bütschli (1873) showed that this division was unwarranted, and so the term must be rejected.

Cognizant of the fact that there were forms in which the muscle cells because of their great variation could not be accurately placed in either the group of Platymyarians or Coelomyarians, and further that some worms were found in which the cells were different in different parts of the body, Schneider (1863) proposed to abandon these original names and use instead Polymyarii and Meromyarii, basing his classification on the number of cells that appear in a cross section. In the former, as the name signifies, many cells occur, in the latter there are only eight, or two in each quadrant.

It is evident that *C. americanus* is a Polymyarian on this basis and on the dividing line as regards the original groups. *Ancylostoma duodenale* stands about on the level with the new species as regards the type of cell, but is a Meromyrian according to the division of 1866.

A discussion of the advisability of continuing this classification will be found in the section on systematic position of the form, but it is interesting to note here that Martini (1909) states that all Polymyarians studied by him have many cells in a cross section of the gut, but, while there are many Meromyarians with an intestine composed of only two rows of cells, there are those in which the intestine has as many cells in cross section as in any Polymyarian, e.g., Oxyuris.

SPECIAL MUSCLES

The intestinal muscles. The intestinal muscles (dilators) in the female arise about 0.4 mm. from the anterior end of the rectum and extend to that level. They arise as four separate bundles of fibers, each about 7 μ in diameter. After a rather long insertion on the inner side of the cuticula, pass down diagonally thru the body cavity to run posteriorly along the side of the intestine, one at each "corner," so that they lie, two in the dorso-lateral and two in the ventro-lateral fields (Fig. 118). Their anterior insertions are in each quadrant just between the first muscle cell to the dorsum or ventrum of the lateral lines and the lines themselves.

About half way in their course each dorsal bundle unites with a ventral bundle on the same side (Fig. 129), so that there is a widened

region on each side of the intestine, curving around it in the shape of a horse-show. It is in this widened region, on either side, that a single nucleus is found, lying towards the dorsal side of the place of fusion. This demonstrates that each lateral pair of fiber bundles belongs to one cell, which branches anteriorly into two parts. Below this anastomosis of the two bundles, each cell branches out (Fig. 120) and these fine divisions become attached to the outer wall of the intestine. When the branches become as numerous as ten, there is seen covering all of the branches and enclosing the intestine, a thin fibrous tube (Fig. 123), which binds these smaller bundles of the intestinal muscle cells to the intestine. This tube of fibrous material extends to and is continuous with the fibrous element of the sphincter muscle cells, becoming along its course much thicker than at its beginning. Near this region there appear two nuclei, one of which is always more posterior and lies a little to the left of the mid-ventral line, (Fig. 125). The outer varies in position but is usually dorsal in location (Fig. 126). In the section on the rectum a more complete account of these structure will be given, but here a few words are necessary. Looss has not mentioned the existence of such a fibrous tube as here described, but has stated that there is a sphincter, muscle composed of a small number of fibers and a single nucleus in Ancylostoma. It seems probable that this tube here described in reality is the sphincter, greatly developed and serving as a means of effecting a good insertion for the intestinal muscles, as well as for the constriction of the lower portion of the gut. The second nucleus may have been overlooked by Looss or may be present in *C. americanus* on account of the greater development of the sphincter.

Branches from this tube pass over to the ventral line and some few to the lateral lines, and undoubtedly carry in them the nerves to supply this structure. Just in front of the rectum one can count as many as thirty-five branches spreading out all around the intestine, and these are held in place by the fibrous tube, and partly, by the fusion to the gut wall in the very posterior region.

As to the function of these fibers which go to the intestine a word should be added based on their position and insertion. I believe that they oppose the anal muscles in part and the sphincter muscle as well. Their contraction would raise the intestine and at the same time expand its lumen, the anal muscles by contraction would pull

down the gut into position and the sphincter would close it. The sudden elevation of the gut and expansion of the lumen would of course act to expel the intestinal contents. There is no evidence to show that peristaltic movements occur in the guts of nematodes.

A continued contraction of these muscles would tend to inroll the tail, a fact taken into account in the discussion of the musculus ani. Looss states that the branches of these muscles which partly encircle the gut in *A. duodenale*, by contraction would not only open but also close the gut, an action which would be hard to conceive in any case, much less in *C. americanus*. In Ascaris these muscles are so placed that it would be impossible for them to close the gut, for here branches radiate all the way around the intestine and are inserted on the cuticula (Voltzenlogel, 1902).

In the males, the intestinal muscles are not so well developed as they are in the females, and are much shorter. They are anteriorly inserted a little above the level of the beginning of the caudal muscles and have their posterior insertions effected by branching out over the intestine just above the rectum. However, the branches are by no means so numerous as in the case of the females.

Musculus ani. Altho Looss described this muscle correctly he called it "musculi anales" for which I can see no justification, since it is clearly one muscle and furthermore composed of one cell, which fact Looss points out; no one would speak of a biceps as being "muscles" simply because it has two places of origin.

This muscle is present in the females only and is in the shape of a fan, spreading out antero-posteriorly as well as laterally. One insertion of this muscle is along the dorsal side of the rectum in its posterior sixth, immediately above the anus. From here it spreads out in all directions, (Figs. 8, 113, 119), but with the main divisions running on the right and left sides of the body, these in turn break up into branches which are inserted on the inner side of the cuticula between the regular somatic muscles. Previous authors have called attention to the peculiar shape of this muscle, which is roughly that of the letter H, for between the two places of insertion there occurs a narrow strip of sarcoplasm in which is present a large spherical nucleus (Figs. 113, 119), demonstrating that the structure is really composed of a single median cell.

The action of this muscle has been indicated in the section on the intestinal muscles, and only a word need be added here. When the gut is elevated and opened by the latter muscles, the body is inrolled to some extent, this being true when the feces are expelled, when the musculus ani contracts, its broad outer insertion allows it not only to pull the gut down into place but to straighten out the tail as well. Thus these two sets of muscles are even more closely related to the general somatic muscle cells in function than has been suggested by previous authors. The function of this cell is taken over in the male by the modified caudal somatic muscle cells.

The Digestive Tract

Altho the *oral apparatus* of the genus *Camallanus* is so very characteristic and prominent, none of the previous writers have given good descriptions of the parts or have interpreted their functions aright.

The earliest description which was available to the author was that of Rudolphi (1809) who wrote of the structure in the following manner: The mouth (the principal food passageway) is globular and longitudinally densely striated, with a posterior apophysis, short and extending transversely, which seems to end in two short internal hooks, obtuse and incurved. There are two other external, longer and decurrent ones; or if the total apparatus (vasa) is short, the hooks seem to be set into the intestine. As for the shell (cucullum) itself, it does not entirely fill up the body, a part is empty and appears clear, which is called the clear spot (macula pellucida), a peculiar organ but not considered.

The next author to describe the structure was Dujardin (1845) and his meager account of the apparatus of manducation is that it is formed of a shell, with a short transverse bar at its base, and two intermediate pieces forming a longitudinal body with two or four divergent, oblique and posteriorly directed branches.

In Schneider's monograph (1866) appears the following description: The mouth is slit right and left, occupying the entire region of the head; it is built into a thick capsule, somewhat elliptical, more circular posteriorly and opening into the esophagus in a cross-shaped opening. On the internal surface of the capsule occur a number of ridges or teeth, parallel and forming small teeth on the margin of the

buccal orifice. The sides of the capsule are not equally thick; in the anterior part of each side, they are reduced to a thin membrane. The dorsal and ventral portions, which are brown and thick, give to the eye the appearance of two opposed shells. Behind the capsule, on each side, one sees an apparatus of three branches, made of the same substance and continuous with the shells. These prolongations are morphologically, and without doubt physiologically, of the same nature as the apparatus with the three branches in *Filaria pungens*, which they resemble. The trifurcated apparatus is situated, not in the esophagus, but outside of it.

Perrier's description (1872) is more lengthy and while superficial and incorrect in some respects, gives the best idea of the structure. His figures are copied in Plate XVI. He writes: In the first place the two buccal valves are very evident and are not simple in appearance, due to the thickening of certain parts of the capsule, analogous to the cephalic capsule of the strongyles and related Nematoda. These valves are perhaps joined to each other by a ligament as different bones are joined; no one would consider two adjoining bones as having been formed at one and the same time, so in the case of the capsular articulation. I believe that the formulation of the opinion of our adversary of the present moment, Schneider, allows the entertainment of strange, preconceived, morphological ideas held in regards this genus and the strongyles.

Each valve is composed of a part, more or less semi-elliptical, concave towards the interior and situated anterior to the esophagus: it is the active part of the mouth; inferiorly this part is prolonged into a sort of median point, rectangular, short, somewhat transparent, and engaged in the esophagus where one can easily distinguish it. On each side, the two valves are separated, the one from the other, by a chitinous nodule on which they are simply supported by their inferior angles, and is not made in so sharp a fashion as the body of the valves; on the inferior side this nodule rests on the superior margin of the esophagus. It gives origin to two kinds of chitinous structures:

(1) Three lateral branches which are spoken of by other authors.

(2) Two transverse chitinous bands, a superior one, and a ventral inferior one.

These chitinous bands unite the two nodules, making an absolutely firm contour. Each band is formed of three parts, of which

the two laterals are convex towards the exterior, while the middle scallop, weaker and less colored than the other two, is convex towards the interior and supported at its summit on the middle of the inferior border of the corresponding valve.

These are the analogues of the two chitinous bands, which Rudolphi wished to call the apophysis, as he designated this transverse bar. Unfortunately, the peculiarities presented by this bar in the species under discussion are not recognized, and its physiological rôle has completely escaped helminthologists in illustrations, as it has escaped those who have occupied themselves with the form from the perch only.

The lateral branches are three in number on each side; with a length of 60 μ. Of these branches one is median and unpaired on each side; the other two are symmetrical and formed in consequence of a sort of angle which the median branch bisects. This last branch is straight, pointed at its summit, oblique from before and behind, and from within outwards, in respect to the axis of the body; it is found immediately in contact with the sides of the body, which it serves to support. The other two branches are strongly curved and divergent, one is high and interior, the other low and largely exterior. It is a little underneath their junction with the chitinous nodule from which the apophysis arises. Each of these nodules terminates in a large swelling of chitin, in which is inserted a large muscular cord, which passes from before backwards and from without inwards towards the axis of the body. One can distinguish very clearly four muscular cords among the longitudinal muscles of the body and among the cords which unite with the esophagus, with the sides of the body and the chitinous branches themselves.

Perrier thought that if the muscles attached to the posterior tips of the prongs should contract, they would tend to pull together the posterior tips and because the middle scallop was weak it would give in, allowing the anterior margins of the valves to be sprung open. When these muscles were relaxed the simple elasticity of the material, it being under compression, would cause it to resume its normal shape. Outside of this explanation, which will be shown to be totally incorrect, there is in literature no explanation of the action of these parts, so far as my information goes. Before going into that it is necessary to give a full account of the exact morphology of the parts of the

oral region. Judging from either the text or the figures of the earlier authors, there is some confusion as to the position of the two lateral valves, as I shall designate the most prominent structures of the mouth region. Altho it is difficult to tell from the poor figures given by Rudolphi, and there is no statement in the text, it seems probably that he considered the valves as being dorso-ventral in position. Schneider and Perrier certainly considered them as being in this position as well as does von Linstow (1909), if one is to judge from his figures. Railliet and Henry (1915a) give as a generic character the position of the valves, which they state is dorso-ventral. Dujardin, Seurat (1915a) and Ward and Magath (1917) have correctly stated that they are lateral, and with this view I agree: reference to the figures and descriptions will prove this contention.

Authors have applied various terms to the description of these valves; some are: kappenförmigen Mundkapsel (Goeze 1782), cucullo striato (Rudolphi), coquille (chaperon cucullus Rud.) (Dujardin), valves buccales (Perrier), camail d'apiculteur (Railliet and Henry) and Seurat refers to them as being "buccal valves shaped like the valves of pecten." This last phrase very nearly describes them, for as viewed from the side they present a very close resemblance to such shells, except they are a little more convex (Figs. 1, 2, 3, 4). These two valves, of which one is a right and one left, are united in their posterior half; a cross section in this region shows a complete, rather oval-shaped structure of valve substance, (Figs. 13, 16). A section taken more anteriorly shows they are free of each other, and appear as two jaws (Figs. 12, 15). The whole apparatus is a golden brown color. These valves appear longitudinally striated which is due to the presence of ridges projecting a few micra towards the interior. The number of ridges varies a little in different specimens and in the regions of the valves, so that a section taken near the posterior region will show six ridges and as the sections are examined anteriorly more ridges make their appearance until there are ten or twelve in all, divided into two fields, so that there is a little distance in the middle in which there are no ridges. Near the anterior margin of the valves these ridges suddenly increase in depth so that the end shows little hooks formed which project out into the buccal cavity as rather sharp teeth (Fig. 12). The anterior median margin of the valves is notched in the shape of a U. From either side of this

notch the anterior margins pass off in a slight curve, which proceed posteriorly and dorso-ventrally; at the point where the valves are united to each other is the widest part of the jaws, it being in each female 0.16 mm. and 0.12 mm. in each of the males. Another curve which forms the posterior and lateral margin of the valves passes posteriorly and to the mid-lateral lines; it is along this line that the two valves are united. Posteriorly (Fig. 14) there is a round hole which opens into the esophagus. The valves are made up of two layers, varying in thickness in different regions but around 7 μ, except along the line of union where they are half so thick. Length: in the males, 0.089 mm., in females, 0.105 mm.

Around this posterior hole is placed a ring (Figs. 1, 4, 24, 34) which is made of the same substance as the valves, as all other parts seem to be. This ring is thin and curved so as to fit down over the anterior margin of the esophagus. It is about 0.1 mm. in diameter, and is rather tightly joined to the valves but can be parted with a needle and then breaks off smoothly. In the fourth stage the ring is formed, but appears more curved over the esophagus, perhaps when growth of the esophagus takes place it pushes the ring up and straightens it out, at least it gives one that impression.

Both of these parts described lie well within the body of the worm and nowhere do they touch the cuticula save at the most anterior margin, where the valves are in contact with the inner margin of the thinned cuticula which runs up just over the edge of the valves to end on a level with their inner surfaces, and again at the widest place in the valves (Figs. 17, 19).

The third important structures of the oral region are two sets of three posteriorly directed spikes (Figs. 1, 2, 18) known as the tridents. These lie one dorsal and the other ventral in position with the posterior ends radiating out, so that the total amount of circumference included between the points of each set in over one-fourth of the total circumference of the animals body in that region. Each of the tridents is constructed as follows: The anterior margins of the three spikes are brought together into a solid nodule which is hollowed out on the interior and fits over the region of the valves where they are united, this articulation looks very much like that made by the humerus with the scapula and may be spoken of as a ball and socket joint, however the juncture must be well made because it is not an

easy task to separate them from the valves, except by special treatment. From this socket the three spikes radiate and about half way of their length push into the cuticula itself, so that they lie for the rest of their way in the cuticula, between the two chief divisions, the points firmly embedded within it (Figs. 46-49). The middle spike runs exactly mid-dorsal or ventral, as the case may be, and is nearly square in cross section, coming to a point at its posterior tip, and being in the males 0.08 mm. long and in the females 0.05 mm. The two lateral ones are almost oval in cross section and have a slight swelling on their posterior ends; they are about the same length as the middle ones.

Two other kinds of structures are present in this complicated apparatus. The first of these to be mentioned are the so-called papillae of the earlier authors, and here called the anterior wings (Figs. 1, 2, 4, 15, 22, 23). These are a right and left pair firmly attached to either valve just posterior to the anterior margin. Each wing is attached by its inner margin to the valve and the rest is free, extending laterally for a distance of four to six micra. Their shape is roughly that of the wings of a beetle and are drawn from a top view and slightly stretched out in the figures. They are about one micron wide.

The last structure to be described is the pair of valve covers (Fig. 20) never before referred to in literature. There is one to cover each valve and is triangular in shape, with the apex rounded, mediananally notched and placed anteriorly. The whole structure is very thin, but apparently made of the same material as the rest of the apparatus. The sides as well as the base are curved inwards. The two basal corners are pointed and are weakly attached to the inner margin of the socket of each trident. The anterior margin is strongly attached to the anterior outer region of the valves, just below the insertion of the wings. The covers are curved to fit, and lie closely applied to the outer surface of the valves.

If worms are treated with concentrated caustic alkalies the entire worm, including the cuticula is dissolved on standing, or immediately on boiling, except the mouth apparatus. This remains intact so long as strong currents do not break it up into its several parts. The easiest parts to come off and those which do so first are the tridents, then the covers, then the ring. The wings and the two valves always

remain intact and none of the parts dissolve so far as can be detected with the aid of the microscope. It should be said that while the head parts have been kept for days in very hot alkalis they have never been boiled in experimental tests, since they are so small that it is not practical to recover them after such radical treatment. It seems evident enough then that the oral parts are not of the same substance as the cuticula. The fact that they are not soluble in hot concentrated alkalis is quite suggestive, as this is one of the chief characteristics of chitin. Every known test for chitin has been tried on these structures and each gave negative results, but since these structures are so deeply colored, I am under the impression that should the purple tint be formed it could not be recognized. Until enough material can be obtained to make a chemical analysis I cannot say what the substance really is. The only absolute way that could be used to show this apparatus was made of chitin would be to isolate glucoseaminehydrochlorid from it and this is impossible with the present method known. The fact that it is soluable in acids makes it certain that it is not keratin, and considering its color and the fact that it is insoluble in concentrated alkalis, it seems rather probable that it is made of chitin.

The last point of interest is how does the apparatus operate and what is the physiological significance of the whole as well as the parts? In beginning this answer it is necessary to look at the pathological picture presented in the intestine of the host. If the intestine is sectioned with worms still attached it will be seen that the ability to hold onto the wall is developed to a great extent, which fact is observed in nature when they are pulled off of the gut for study or preservation; the amount of traction necessary to dislodge them is remarkable. Within the mouth and filling up nearly the whole cavity will be found a plug of intestinal mucosa Figs. 132, 133 the shape of the oral cavity. Where the plug is in contact with the rest of the wall, the cells show a great degree of distal suction-result, so that they are compressed and the nuclei drawn towards the plug. No marked edema seems to occur at the foci and comparatively little accumulation of leucocytes. At the proximal end of the plug, the end hooks of the internal valvular ridges are seen firmly embedded in the tissue.

If a worm is taken from the wall of the intestine and placed with a piece of the gut under a binocular and watched, it will be seen to go thru very characteristic motions which finally result in its attachment to the wall. Sometimes this will take place within a few seconds and the jaws can be seen to open and close; a motion can be observed whereby the jaws are made to rock upon the tridents. The power of motion and the ability of the jaws to attach themselves to the intestinal wall is due to the presence of a right and left pair of muscles (see figures of mouth parts), each composed of two cells, so that there are four cells in all. In addition to this there is the fact that the jaws are kept from being pushed posteriorly by the firm attachment of the tridents and the fact that there is a powerful suction exerted upon the tissue by the esophagus.

These four muscle cells have the following positions and take their names from this fact: right dorsal and ventral and left dorsal and ventral. The anterior insertions of these is at the anterior margin of the valves, where there is yet no sarcoplasmic process and where they are closely applied to the wings, which help in supplying insertion surface. Here the fibrillar portion is in contact with the wings and the valves on the one hand, and with the cuticula on the other, the muscles being between the cuticula and the valves. Just below the attachment of fibrillar portion of the muscles, they break away and thus the most anterior part of the valves is the only place of insertion, this gives more leverage as will be seen later. The sarcoplasmic portion appears between the fibrillar portion and the jaws, and the nuclei of each cell is seen on about the level of the buccal ring. These muscles extend down the lateral margins on either side of the very narrow lateral lines, the sarcoplasmic portion extending a little below the nerve ring and to the level of the lateral cervical ganglia. The fibrillar portion continues only to the nerve ring. These cells are enormous as compared with the other muscles of the body, they being 0.08 mm. wide and the sarcoplasmic process being 0.03 mm. in thickness.

Being longitudinal muscles, on contraction they pull the anterior margin of the valves open, because the tridents prevent any backward traction, being firmly held in the cuticula. The thinning of the valves at the line of juncture, and the fact that they are convex provides a lever which is made use of by these muscles. If only one pair of the

muscles is contracted the valves will rock upon the tridents and this motion orients the mouth with respect to the gut wall. Thus attachment is made by the rocking of the valves to get the mouth in position, correlated contraction of the two pairs of muscles to open the jaws, suction by the esophagus, and relaxation of the muscles when a portion of the gut is in the mouth. Of course the normal motion of the worm's body helps to keep the mouth in close contact with the intestinal wall. Once the mouth surround a plug of tissue, the hold is made more effective by the anterior hooks, for these work somewhat like the barbs on fish-hooks. The only function of the ring seems to be that of support, for it furnishes a large surface to fit over the end of the esophagus.

It would seem then that the explanation of Perrier is in error, chiefly from the fact that he was ignorant of the exact structure of the parts of the oral apparatus. The prongs are not connected to a "middle bar," but the "ring" really belongs to the valves, is well joined to them and is developed before the tridents. The tridents when they are developed come from a region at the extreme lateral margins of the valves and not from this ring. In the next place there are no muscles connected to the ends of the spikes of the tridents, an error carried by Railliet and Henry even in 1915. These are so firmly embedded in the cuticula that they are not capable of motion and by this very fact make it possible for other parts to move. The restoration of the apparatus after opening is in truth due to the elasticity of the structure, but not to "the middle of three scallops" which do not exist, but to the elasticity along the line of union of the valves.

Some other points regarding this interesting mouth apparatus in particular as regards its condition in young specimens, will be discussed in other sections of the paper, to which the reader is referred.

The esophagus. The esophagus of nematodes has been suggested by previous authors to be of importance both from a phylogenetic and an ontogenetic standpoint. This type of esophagus has been said by many to be characteristic of the group of Nematoda, and so far only one kind of exception has been found, and that in the division made by Ward (1917) as the Trichosyringata. In this group the esophagus is a capillary tube, enclosed within a row of cells, a condition which is not very well understood. The fact that in certain species at least, the esophagus reaches a maximum length early in

the growth of the individual, makes this organ of some value in identification and its constancy within a given genus shows that it is subject to little variation thruout different species within a genus. Taking it all in all it seems that the esophagus should be considered as a very important organ in the nematodes, and its shape, size and structure should be given in descriptions of these animals.

In *C. americanus* there exist two portions of this interesting organ (Fig. 3), which divisions are called the anterior and the posterior parts or regions. As evidence for considering these two regions as belonging to one structure, I offer the following considerations:

(1) The outside covering, the tunica propria, covers both regions as a continuous structure.

(2) The inside lining is of the same structure and substance and continuous; it is tripartite in both.

(3) The muscles and nuclei are arranged alike and have similar histological elements in both regions.

(4) No valve exists between the anterior and posterior regions.

(5) There is a typical valve between the posterior margin of the posterior portion and the intestine, just as found in all other nematodes studied for this particular structure.

(6) The dorsal gland is continuous in both regions.

The use of the expression "first and second esophagus" is misleading and is on the whole unfortunate.

The anterior portion, to follow Cobb's (1898) nomenclature, is conoid in shape but expanding very gradually towards the posterior portion, until it is about as thick as anteriorly; rounding off, it presents a nearly straight margin where the posterior portion begins (Fig. 3). There is no evidence that esophageal torsion exists in this species as in the case of *A. duodenale.*

This region is lined thruout with a substance similar in appearance and staining reactions with the cuticula and it, like the latter, dissolves in alkalis; in these facts it offers some evidence for considering it as being formed by the invagination of the external cuticula as most authors have held. Owing to its size and position I have been unable to obtain enough of it for an analysis. Its solubility in alkalis and its failure to respond to a chitin test removes it from consideration there, altho nearly all authors have called it a "chitinous lining." Anteriorly the lining is in the shape of a circular layer, and narrows

down like a funnel, until a few micra posterior to its anterior opening, which is within the field of the mouth apparatus ring, it changes into a triradiate shape and encloses a very small cavity. This "funnel" (Looss 1905) is composed of a substance which is continuous with the rest of the lining (Fig. 34), altho it appears set off from it, staining very deeply and being much thicker. Anteriorly it abuts on the lower margin of the jaws, as tho it was at one time continuous with them also. This region of the lining seems to act as a cap for the anterior portion of the esophagus as well as a lining. From here on the lining is triradiate and six thickening appear, two on each third, and at the center of each field. They are oblong in cross section, and are like ridges extending almost the entire length of the anterior portion of the esophagus. The lining is further thickened at the juncture of each side, this acting as a hinge for opening and closing the lumen. These thickings get larger posteriorly and just before the beginning of the posterior region they become smaller, disappearing entirely 15 μ anterior to this level; the triradiate lumen continues then to the posterior margin of the esophagus (Figs. 41 to 45 give a series of views of the lining, drawn on the same scale).

The marginal thickenings are for the insertions of the marginal muscles (called so by Looss, 1905) as well as serving for a hinge, and these muscles appear as a small group stretching out from this inner insertion to the tunica propria. The nuclei of these cells lie in groups of three at the same level and there are two such groups, so that six nuclei are found in these muscles. The protoplasmic strands with them are sarcoplasmic, and the nuclei lie half way between their two insertions.

The other set of thickenings are for the insertion of the ordinary muscles of the esophagus, which are more numerous than the marginal fibers and usually stain a little darker. Their nuclei appear in groups of six at one level, two nuclei in each field; being three groups, there are in all eighteen nuclei for these muscles. The marginal and the ordinary muscle cell nuclei alternate with each other thruout the entire esophagus. The latter nuclei lie a bit more peripherally than the former, in most cases. The sarcoplasm of these cells is more abundant than in the marginal muscle cells (see Figs. 30, 47, 49 for the structure of this region of the esophagus).

A gland lies in the dorsal third of the esophagus, which will be discussed later.

The action of the esophageal muscle cells is obvious. Their contraction opens the lumen and in living specimens this can be seen, and that the entire lumen opens at once. The elasticity of the lining closes the opening. The marginal muscle cells keep the lumen in position and so have a kind of supportive function as well as helping in the opening process.

The posterior region of the esophagus is made up of a different looking tissue than that found in the anterior portion. The general shape of this region, which is cylindrical, is shown in Figure 18 where it can be seen to be of nearly equal diameter thruout, being slightly swollen in the anterior region and expanding up to its widest parts from a narrowed portion just behind the anterior enlargement.

The tunica propria of the anterior portion of the esophagus extends over the posterior portion, somewhat invading the tissue between the two regions, serving to set them off from each other (Fig. 40). The lumen of the two regions, as has been remarked before, is continuous, the characteristic lining of the anterior portion giving way to a simple triparted lining with no special places for the insertions of muscles in the posterior region. This lining extends to the end of the valve.

Four different kinds of tissue can be recognized in this region of the esophagus.

(1) The sarcoplasm of the dorsal esophageal gland, with its single nucleus, will be treated under a separate division of the paper.

(2) The second tissue is of a nature not greatly unlike the muscle cells of the anterior portion, and I consider it to be weakly developed muscles for the opening of the posterior lumen of the esophagus. In this tissue can be seen small nuclei (Fig. 31), with a single nucleus in each, near the lumen and therefore near the insertion of the muscle fibers of the ordinary muscle cells; there are also marginal nuclei. The arrangement of these nuclei follow the general rule of the anterior portion. Just posterior to the anterior tissue cone (see below) there is a set of three marginal muscle nuclei, further down there is a group of six nuclei, two in each field; posterior to these appear another group of three marginal nuclei and then the number and arrangement is not, so far as I could find, constant in the individuals examined. There are usually several (2 to 6) scattered nuclei, sometimes apparently marginal and sometimes ordinary muscle nuclei; perhaps

typically there is another group of six, following the general rule, but have been overlooked for some reason.

The ordinary muscle cells are inserted in the middle of each side of esophageal lining and have their outer insertions along the tunica propria, spreading out more like a fan than do the cells of the anterior region. The marginal muscle masses are, as in the anterior portion, inserted at the angles of the lumen. While these two different kinds of fibers are made out in the best preparations and by following thru series of sections, specimens show some variation in the distinctness of these two kinds of fibers, and more than that, there are often insertions of muscles all along the lining of the lumen, with fibers radiating out to the inner side of the tunica. The muscle fibers stain deeply and show a fibrous structure with little or no granular material. There are perhaps no more than twenty nuclei in this tissue.

(3) A third type of tissue is confined to a region in the anterior region of this general part of the esophagus, and is in the shape of an inverted cone (Figs. 40, 39). This tissue, a syncytium, is very granular and stains deeply, lies in the center of the esophagus around the lumen and just posterior to the division between the two regions. There are twelve nuclei within it, three in each of the three fields. These nuclei are a little larger than the muscle nuclei, and each has its nucleolus. There are numerous vacuoles in the esophagus surrounding this plug of tissue and muscle fibers invade some of this region. The function of this region is unknown and no suggestion so far can be advanced until a further study is made of it.

(4) Concerning the last type of tissue I feel more certain. This also is granular in nature and not very closely packed together, is made up of larger granules than in the preceding case, but they stain very lightly. This tissue fills up all the space not occupied by the others so that there is considerably more of this type than all the rest put together. One very interesting fact is its composition of but two cells, their nuclei lying one in each of the two sub-dorsal fields of the esophagus in their posterior tenths (Figs. 3, 33, 38). These nuclei (Fig. 37) are spherical in shape with a spherical nucleolus in each. The nucleoplasm is highly granular and the nuclei stand out sharply as black staining bodies. This tissue, or rather these two cells, I consider to be involved in the excretory function of this animal. There is in the third division (dorsal) anterior to these two nuclei

which are on a level with each other, another large nucleus belonging to the dorsal gland and by comparison with the other two seems to be quite different not only in being smaller but also in being ellipsoidal. In the table below the measurements of these nuclei are given.

	Size	Volume
Gland nucleus	0.0083 x 0.0140 mm.	0.000001182 cmm.
Excretory nucleus	0.0161	0.000002245
Gland nucleolus	0.0050	0.000000065
Excretory nucleolus	0.0061	0.000000108

The histology of this part of the esophagus and the small number of nuclei, prevents it from being considered a gland, but rather favor its being concerned with excretory process, especially when its relation to the rest of the excretory system is considered. Just how the esophagus functions in this process is as yet unknown to me, but from a theoretical standpoint it seems possible to imagine the excretory products of the organs to be passed into the body fluid, and then taken out from here by specific action of the two giant cells of the esophagus, to be given up into the bridge and accessory tissue and finally into the excretory ducts themselves. This would presuppose a discriminating action on the part of the esophagus against the food materials which must be present in the body fluid, but this assumption is not at all unreasonable, since the same thing has been observed in the cells of every plant and animal known.

A rather interesting error is committed by Stephens (1916). He writes: "In others (Cucullanus [now Camallanus], Ascaris, etc.), a tube, the so-called glandular stomach, lined only by epithelial cells, follows behind the muscular esophagus. This glandular stomach is, from its structure, easily distinguished from the midgut, or chyle intestine, which is like-wise cellular." From the foregoing study it is evident that for Camallanus, at least, this statement does not hold true.

Like most, if not all nematodes, this species has a dorsal esophageal gland, but glandular tissue is in no other field of the esophagus. This gland extends from the very posterior margin of the esophagus to within a few micra of the anterior margin of the anterior region.

Anteriorly there is at its beginning an expansion of the glandular tissue which includes most of the entire dorsal field and here a minute

duct from this gland empties into the esophagus in the mid-dorsal region (Fig. 30) between the two dorsal thickenings of the lumen; this duct continues thruout the entire gland, lying in its central region. Posteriorly the gland narrows, occupying an elongated ovoid area in the mid-dorsal line. At the juncture of the two regions of the esophagus the gland narrows greatly but expands in the posterior region. Thruout this region the gland is larger than in the anterior region and here and there can be seen little knob-like projections on either side, but these never extend beyond the area of the dorsal third of the esophagus.

Very near the posterior end of the gland there is a large ellipsoidal nucleus (Figs. 3, 37) with a single spherical nucleolus, their sizes being respectively 0.0083x0.014 and 0.005 in diameter. In some cases the gland seems to extend down into the dorsal member of the esophageal valve.

The sarcoplasm of the gland is rather hard to analyze (Figs. 30, 31, 33, 38, 51). In sections stained with Mallory's connective tissue stain, the gland is colored red, due to the fuschin, while the rest of the tissue in the esophagus is colored from a purple to a deep blue. The gland stains with thionin, as also a little tissue within its immediate neighborhood. In any good preparation of the gland can be seen a structureless outer membrane and an inner granular portion. The granules are large and relatively few, so that there are open spaces within the gland, hence there must be a rather large amount of hyaloplasm present. Around the nucleus the granules are more numerous.

As to the function of the gland, if indeed it be a gland, I can offer no suggestions other than those made by previous authors. These particular worms being blood suckers, suggests an hemolytic or anticoagulative function for this gland, yet the opening of the gland duct is perhaps to far posterior to the mouth to favor this view. It seems more logical to agree with those authors who think this structure is a digestive gland, altho the evidence is by no means plentiful and referring to it as a "salivary gland" is certainly open to criticism.

In most nematodes studies there has been described some kind of a valve between the esophagus and the intestine, and most authors have called it the "esophageal valve." On the contrary Looss (1905, 1911) has claimed that this is really an "intestinal valve" and

is here formed by a telescoping of parts in this region. Lane (1916) states that this is true in the genus Ancylostoma. Looss has even gone so far as to locate four cells in the anterior portion of the intestine of the developing hookworm larvae which he claims give rise to these valves, altho I can find no complete history of these cells given. He (1905:91) bases his claim on the following statement: "The fact that, in the valvular apparatus, as in the intestine which follows it, only two cells appear in cross section, while, in the esophagus, three cells are always found composing such a section, indicates that the whole apparatus is to be regarded as a product of differentiation of the intestine," yet he admits a three-cell arrangement in the rectum. However, he states else where that the inner lining of the valves is continuous with the esophagus and thus "we see," writes the author (page 90), "that the outer tunica propria of the esophagus does *not unite* with its inner lining but that there is a *direct connection* between the tissue of the esophagus and the valves, the connection taking place on their *inner* edges." Even his nuclear counts he admits were made under difficulties and noted considerable variation in their number and position.

In *C. americanus* there exists at the posterior margin of the posterior part of the esophagus a structure which I wish to call the "esophageal valve." This structure is remarkably like that described by Looss for *A. duodenale*. It is composed of three valvular projections (Figs. 38, 36) which are well in the lumen of the intestine. Each projection is composed of the muscular tissue of the esophagus plus its own cell which is granular and stains lightly. Each third possesses a nucleus of medium size which can be seen in good preparations. Around the three members of the valve there is a sphincter muscle, containing one or two nuclei (Fig. 36). The cells of the intestine come up around the valves covering the grooves round their bases but *do not cover their free margins*; these project in the gut lumen. The lining of these members is continuous with the esophageal lining and they are somewhat set off by its invasion between the esophagus and the valve, which is not so complete as to cut it off. Each projection represents the most posterior part of its respective third of the esophagus.

I can see no justification for assuming, in *C. americanus* at least, that this valve is intestinal, and on the other hand very good ground for

believing that it is an esophageal structure. In this I agree with Cobb (1898), Quack (1913), Railliet and Henry (1915), Lane (1916a) and others. The fact that the cells are continuous with the esophageal syncytium, that they are lined with the continuous layer of the esophagus, and covered with the same tunica propria, are three in number and with a nucleus in each, that they are set off from the intestine and of entirely different histological structure, and finally that they function to prevent the backflow of food into the esophagus points to their belonging to this organ rather than to the intestine.

Leuckart (1876) in his work on the life history of *Camallanus lacustris*, figures a group of cells at the posterior region of the esophagus which he found to develop into this valve like structure in that species. This, of course is additional proof for considering this valve of esophageal origin, for one would not expect the conditions to differ in the same genus.

It is difficult to believe that this valve is not homologous with that in Ancylostoma and the other nematodes, and yet if Looss be correct, this could hardly be true. I have been unable to convince myself either by a study of the text or his figures, that in the form described by Looss, this valve is intestinal, and his failure to find the third nucleus in the third valve member (he does not say in which projection this was lacking, nor is he clear that it is always lacking in a particular one) I consider due to his technique, and the condition of the tissue at the time of killing and fixing. He admits his difficult-ties in counting the nuclei in this region, which has been noted above for the posterior region of the esophagus and these are often very near the valve itself in contracted specimens, so that the chance for confusion is greatly increased. After all, in *C. americanus* there may be more than three nuclei concerned with this valve, but at least there is one in each division. If Looss be correct in his statement that the "two-cell" condition is carried in both the valve and the intestine, on this reasoning one would expect many more nuclei than it would be possible to have in the valves, because in *C. americanus* there are many nuclei in cross section of the gut and in some forms, there would be even more.

I am forced to the conclusion, therefore, that the valves of various nematodes are homologous and are specializations of the posterior portion of the esophagus; that the cells of the intestine have crept

up around their bases and a sphincter muscle has been developed out of the intermediate edges of the tissue, perhaps in part from both, or entirely from either one. This conclusion seems warranted from a study of the present literature, although subsequent study may show that there is here a fundamental distinction between certain nematodes.

The intestine. The portion of the alimentary tract which lie between the esophagus and the rectum is known as the intestine, or chyle intestine, an unfortunate name, since there are no villi in nematodes.

In *Camallanus americanus* this portion of the tract is made up of tall, hexagonal, columnar epithelial cells. The inside of the gut is not smooth in cross section, but is thrown into irregular low folds. In some nematodes the inside of the gut is very smooth, in others there are definite and very deep folds. In adults the cell walls usually break down to some extent, so that often none can be seen, and with this degeneration comes an apparent degeneration of the nuclei (Ehrlich 1909). As in most nematodes, there are definite regions in the cells. On the outside is a thick basal membrane and just inside of this a slightly thickened portion or layer of sarcoplasm.

Towards the center of the cells are numerous reddish-brown concretions or granules (Figs. 60, 115), about one micron in diameter, more numerous in the older individuals than in the young, and chiefly in the anterior part of the gut. Such concretions have attracted the attention of many students of other species and by nearly all are thought to be excretory products of some nature (Exkretkörnen). Looss (1905) describes them for *A. duodenale*, but here they are far less numerous than in *C. americanus*, where they more often than not almost fill the cells. Looss considered them as some product of blood digestion, which seems very logical and would therefore represent what are sometimes termed "coffee-grounds" in human pathology. These bodies are probably a part, at least, of the pigment group of the turtle's blood corpuscles.

In Ascaris this same kind of material has been noted and studied to some extent by Flury (1912) and Fauré-Fremiet (1913). The latter found them to be insoluble in the solvents of fats and resistant to digestion with pepsin and trypsin. He expresses his belief in the following words: "Il est donc tout a fait probable que ces grains

sont l'exprèssion ce la transformation d'une partie appréciable de l'hemaglobine ingerée par l'Ascaris." I am inclined to think that they are not excreted in the form in which they appear in the gut wall, because they have never been found free in the lumen, and they accumulate with the increasing age of the worms, so that very often they are nearly or totally lacking from the intestines of young animals. However, this fact must be kept in mind; the body fluid is colored red, and this color most likely comes from the blood of the host. It may be that these pigment bodies represent stored up material in the walls of the gut, and that they are intermediate products in metabolism; they would then be changed into a fluid, giving the red color to it. Thus some of the material might be used as food, or it may be that parts are excreted, even before being used for food, passing out through the excretory duct. (See the section on the body fluid for a further discussion of this problem).

Among others who have noted the presence of non-cellular materials in the intestines of nematodes Cobb (1914) should be mentioned. He called attention to "rhabditin" in the intestinal cells of *Rhabditis monhystera*, and came to the conclusion, after his very brief study of the material, that it was a carbohydrate, basing his conclusion on the following results: slowly soluble in water, rapidly so in alkalis and acids; insoluble in most organic solvents; the aqueous solution gives no precipitate with barium salts; the substance does not stain with iodin-potassium iodide solution, and the crushed bodies of the worms gave a Fehling's reduction; no trace of the substance remained when the bodies were burned, a faint flicker over the sodium line of the spectrum indicated to him the absence of the earthly constituents that might be expected in certain excretory salts, such as calcium. It is unfortunate that he saw fit to name this substance without more knowledge of its nature. Of course his Fehling's test was absurd, since the bodies of nearly every animal will give a reduction with this agent, especially nematodes, and he indicated no way whatsoever of telling that these granules played a part in the reduction. The failure to stain with iodine solution certainly excludes a great many carbohydrates. It is impossible to tell just what he really had from the very meager information given in his paper, and since he does not refer to any special work on the subject one is inclined to think that he did not consult these particular articles. One of the most recent

and thoro is that of Marie Quack (1913), who concludes that certain granules, which agree in description very closely with "rhabdtin" and found in free-living and parasitic nematodes, are calcium salts, and her evidence in very conclusive on that point. However, these "Sphaerokristallen" are insoluble in water, alkalis and dilute acids. Until Cobb publishes a more complete account of his work one is forced to discount his conclusions, at least one cannot accept his name without better justification from a chemical standpoint.

The nutritional zone (nutritorishe Zone) can be recognized as the layer of thickened protoplasm on the inner border of the cells and inside of this another membrane. The "Stäbschensaume" is very tall in this species, being nearly equal to the height of the cells themselves. In young specimens, this layer shows very clearly its arrangement. Each cell bears a definite clump of little bristles, which proceed from each cell towards the lumen of the gut. In the older individuals these bristles become matted together so that the layer seems almost like a continuous one. Many authors have called this a "chitinous layer," but this is not the nature of the material of which it is composed for Quack has shown that it is digested by the action of pepsin and is soluble in caustic alkalis.

The nuclei of the intestinal cells are ellipsoidal in shape, with a single nucleolus in each, and lie either within the nutritional zone or immediately below it. This position is unusual, for the intestinal cell nuclei usually are said to be well in the middle of the cells, or more typically near the outer margins. Supporting fibers can be seen in the best preparations, stretching out from a slightly thickened area around the nuclei.

Just anterior to the rectum the intestine shows a very poorly developed valve (Figs. 116, 125, 126). The appearance is that of certain cells being pushed up and in posteriorly, so that a small pocket is formed and the lumen is made smaller. The nuclei are very numerous in this region.

The rectum and cloaca. Between the posterior end of the intestine and the anus there is a small region known, in nematode anatomy, as the rectum. The region has excited the interest of workers in the field, chiefly because of certain bodies which always seem to be present, even in the most diverse forms. Various functions have been ascribed to these organs, which are considered to be a group

of three or four cells. Leuckart, Cobb and others have called them "anal glands," but none have been able to propose a logical function for glands in this region of the alimentary tract, since a secretion poured out by them would pass into a cuticula-lined canal and right at the opening of the tract to the exterior. In addition to this, the demonstration of ducts from these cells is by no means certain. Others have spoken of them as "giant cells" and "ganglion cells." Looss could not convince himself that these explanations would explain the function of such cells and finally came to the conclusion that they were cells which belonged to a syncytium of connective tissue in the forms in which he studied the structure, and that "the structure to which they are attached is a ligament for fastening the chyle intestine to the rectum." Before giving my interpretation of the structure, it will be necessary to give in detail the condition found in *C. americanus*. The modification in the males, due to its entrance into the cloaca, makes it necessary to describe the condition in the two sexes separately.

The female. In the females the rectum is a short tube 85 μ long and greatly compressed dorso-ventrally. In the middle region it assumes a slightly triparted shape on the inside and towards the end it shows several prominent excavations or indentations, the largest of which occurs on the ventrum (Fig. 113). Other indentations are shown in Figure 128. Posteriorly the anus terminates the rectum, and is in the shape of a slit (Figs. 113, 114). Where the anus is located the ventral band is divided, its posterior two halves uniting.

The lining is rather thick and as a rule stains more deeply than the cuticula, from which it is supposed to be derived and with which, even in adults, it seems to be continuous, altho the division between the two is usually well marked off. Anteriorly the lining ends abruptly, a few micra posterior to the regular cells of the intestine, and between these two structures is a little space surrounded by three cells, which lie immediately posterior to the lower margin of the intestinal muscle cells.

These three cells (Figs. 8, 114, 127, 128) lie one dorsal and the other two sub-dorsal; they are large and spherical in shape being about 17 μ in diameter. Each spreading out at its base, they form a solid syncytium around the central cavity continuous with the lumen of the gut. Anteriorly these cells pass into the fibrous tube which has

been mentioned previously, and thus they are connected with the sphincter muscle; this fibrous material even extends back over the cells, involving some of their inner and anterior margins. A large spherical nucleus with a single nucleolus is found in each cell. Posterior to these three cells are three others, nearly as large and whose anterior parts push up under the anterior three larger cells, thus replacing them. These cells are not globose but are flattened (Fig. 131), contain large nuclei and each is in one of the three fields as in the case of the other cells. The last three extend almost down to the anus. over the whole of the outer surface of the rectal lining, being rounded out in their peripheral surfaces, they give the rectum the appearance of a regular cylinder (Figs. 130, 131).

The male. In the males this region (Figs. 99, 100) of the gut is essentially like that of the females but of course differs somewhat on account of the modifications caused by the rectum opening into the cloaca rather than at the anus, also on account of the presence in this region of the termination of the male reproductive organs, which become involved with the alimentary tract.

Here as in the case of the female there is a sphincter muscle around the narrowed portion of the posterior end of the intestine and extending just below it, the three giant cells. These cells are not quite so large as in the case of the female and the two sub-dorsal ones are pressed to an almost lateral position on account of the presence of the genital duct lying along the ventrum of the gut. The cells covering the rectum are also present, and these seem to be a part of a syncytium covering the cloaca. The rectal lining is continuous with that of the cloaca. The rectum itself is much shorter than in the females, being only about half so long; it opens on the dorsal side of the cloaca above the opening of the spicular canal.

The cloaca. In the male nematode the common cavity just before the anus which receives the end of the gut and the reproductive organs, is known as the cloaca. This very short passageway is a cuticular lined cavity with an outer cellular covering, containing a few nuclei and part of the syncytium covering the rectum. On the dorsal side, as has been noted above, enters the rectum, and along side of it (Fig. 92) on the ventrum, is found the terminal of the genital duct. Just posterior to the opening of the alimentary canal is seen the opening of the spicular canal. After a short course the cloaca

opens to the exterior in the midventral line as the ano-genital aperture (Fig. 79), 10 μ in diameter and in a slightly elevated portion of the cuticula, on either side of which are the two pairs of para-anal papillae.

The interpretation of these structures in this case is not an easy task and the final word cannot be said until the embryology is known. I consider the posterior three cells described above to be the "posterior ring" cells of Looss, and think they are nothing more than the rectal cells. They may even form the lining of the rectum, their position and granulation would suggest this: at any rate they support it and of course must help to connect up the posterior structures, but I am unable to consider them as being separate parts of a special ligament, as Looss would have one believe the corresponding structure in the hookworm serves. The three anterior and larger cells, are evidently the cells Looss thot made up the "anterior ring" and these are near the region which is supposed to be contracted by the sphincter muscle. Looss admits that there is a very close relationship between the rectal sphincter muscle and the "anterior ring of the rectal ligament," and in reality the two structures seem to be one and the same. The nuclei of the large cells are then in part nuclei of the sphincter, and the globose portions of the cells are the sarcoplasmic parts of the entire structure. The outer parts of the cells are granular in character but the line around which the three cells are united with each other is towards the anterior side, fibrous, and continuous with and exactly like, the circular tube enclosing the posterior portion of the intestine, and which is in reality the rectal sphincter. A contraction of the basal ring of the three cell syncytium serves to close the posterior end of the gut, helped by the action of the tube of fibrous tissue. It is opened by the intestinal muscles, which section see for details. In *C. americanus* the interesting bodies are nothing more nor less than parts of the rectal sphincter. Under this interpretation the two nuclei in the sphincter proper are not well explained, unless they be considered as accessory in nature.

There is some doubt in considering these as purely connective tissue cells as Looss thinks; they serve as such in a way, but the two sets of three cells are better interpreted as separate structures and as given above, at least in this species. From the text and figures of Looss one cannot see that he has, in his own case, demonstrated his

contentions, for he clearly shows that the fibers of the sphincter muscle are "intercalated" among the protoplasm of the three giant cells.

Food. All of the evidence at hand points to the fact that the normal food of this species is the blood of the host. This is indicated by the red color of the body fluid and the pigment in the intestinal walls.

Looss devoted some time to a study of the condition in *A. duodenale* and came to the conclusion that in this species the normal food was not human blood but rather the intestinal mucosal cells. This he demonstrated by the fact that the amounts of pigment varied in different worms and not with their ages and in addition to that, the pathological condition of the intestine of the host and the presence of the intestinal cells in the lumen of the gut of the worms bore out this conclusion.

In the case of *C. americanus* neither of these conditions exists. I have never found host intestinal cells in the guts of these worms nor does the pathological picture in the intestine of the turtle indicate that the intestinal lining was being eaten. The great amount of pigment and the fact that it is found in greatest quantities in the older individuals indicates further, that blood is the normal food of this animal.

From an anatomical standpoint there is further evidence to this effect. The presence of the small sharp hooks at the anterior end of the jaws affords instruments for the laceration of the tissue and the movements of the mouth apparatus are conducive of the same effect. The strong suction made by the action of the muscles of the esophagus serves to draw in blood. The blood corpuscles must be rapidly digested for they are seldomly found within the parasite. All evidence goes to demonstrate that these animals are blood suckers.

An interesting experiment was carried on to see if these worms could be kept alive in a cultural medium and if they would use the medium for food. After several trials a mixture of Witte's peptone and gelatin was obtained so that the warmth of the hand would melt it and at room temperature (about 21 degrees C.) it remained solid. Before the worms were introduced the medium was tested and gave the following properties after sterilization:

(1) Tryptophane present in combination only.

(2) Biuret reaction was positive.
(3) Clear solution, liquid at hand temperature.
(4) Micro Kjeldahl determinations gave the following results:

I. Total nitrogen per cc. 0.0039 gm.
II. Total nitrogen per cc. 0.0042 gm.
I. Non-protein nitrogen per cc. 0.0015 gm.
II. Non-protein nitrogen per cc. 0.0017 gm.
(The trichloracetic acid method was used)
Average total nitrogen per cc. 0.004 gm.
Average non-protein nitrogen per cc. 0.0016 gm.

Six worms were introduced into a flask of this fluid and incubated at 25 degrees C. The worms were first washed thru a liter of steril water in fifty different wash waters, using steril Stendor dishes, and a sterile platinum needle to handle the worms. Every precaution to avoid contamination was exercised. After allowing the worms to remain for six days an examination of the medium was made and a portion of it plated out in agar after twenty-four hours incubation at the same temperature at which the worms were kept. In addition to this a small portion was introduced into another flask of the same medium and kept in the incubator for six days. The medium after the action of the worms showed the following properties:

(1) Tryptophane as before.
(2) Biuret as before.
(3) Clear supernant liquid with a heavy precipitate, but the liquid at temperatures below that of the room did not congeal.
(4) Nitrogen analyses:

I. Total nitrogen per cc. 0.0036 gm.
II. Total nitrogen per cc. 0.0042 gm.
I. Non-protein nitrogen per cc. 0.0033 gm.
II. Non-protein nitrogen per cc. 0.0030 gm.
Average total nitrogen per cc. 0.0039 gm.
Average non-protein nitrogen per cc. 0.0032 gm.

The worms remained alive in this medium for over two months.

The control inoculation was steril at the end of three days and the inoculated medium gave the same results for total and non-protein nitrogen as it did in the original case.

This demonstrated conclusively that these worms can live on other materials perhaps only substances which are like those they get from the blood. Just what they did to the medium was not learned,

but it is evident that they reduced the gelatin to non-protein nitrogen how much further it went could not be investigated on account of insufficient apparatus. This work will form the nucleus of a subsequent investigation to be undertaken by the author.

Worms were kept for two months on turtle blood agar, they being transferred to fresh tubes when the contamination became great. The maximum length of time they can be thus kept was not ascertained in my experiments.

Body Cavity.

For a long time it has been shown that the body cavity of nematodes was not empty but filled with "a fluid probably containing albumen, which curdles under the influence of acid and, when poured into water becomes milky" (Looss 1905:67, translated from Schneider). In the light of modern physiology it seems that the statement of the early investigator of nematodes, Anton Schneider, is by no means incorrect but has an element of suggestion which is probably not far from the truth.

In the absence of a circulatory system and the presence of a large, fluid-filled body cavity, which surrounds the organs, it seems logical to suppose that this acts for the nematode much as does the blood system for other animals; the circulation of the fluid can be seen in living specimens, due to the contortions of the body. If this be true all intermediate metabolic processes and compounds will be found here, and so the digested materials going from the intestine into the organs, and the waste materials from the organs to the esophagus and the excretory ducts will be found, as in other animals, within the same limits and the selection out of the fluid will rest in the power of discrimination of the individual cells.

If one cuts or injures the body wall of an individual of *C. americanus* there runs out of the lesion a quantity of reddish fluid, rather thick and somewhat opaque, which seems to "congeal" within a few minutes. Alcohol and the usual killing and fixing fluids precipitate it and thus it is preserved in sections of worms. Here the fluid appears as a fine granular substance, staining with almost any stain and partially or entirely filling up the space not occupied by the internal organs.

Attempts to obtain hemin crystals from the fresh fluid have been unsuccessful, but the fluid must contain some part at least of the

pigment group of the blood of the host. There is something very suggestive in the presence of the brownish-red granules in the intestinal walls (see that section) and it seems that these granules are in part responsible for the color in the body fluid. The fact that these pigment masses accumulate with the age of the individual indicates that their breaking down process is slow, hence they may be storage products, and the fact that the worms loose their reddish color after remaining for some time in water indicates to some extent that the color of the body fluid comes directly thru the intestine into the body cavity from the digested blood corpuscles, in this event part of the color group would be retained by the gut in the form of the pigment masses in its walls. The whole problem is an important and interesting one and offers possibilities of solution which are more favorable than many others within the same group of worms.

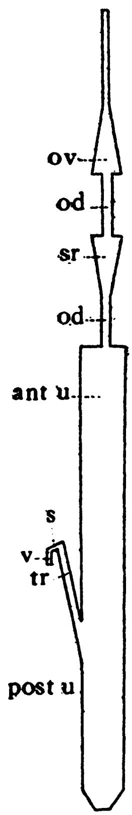
Flury and Fauré-Fremiet (1912) have studied the body fluid of Ascaris and they have found the following substances within it: water, sodium chloride, albumin, globulin, some pure bases, free fatty acids, phosphorous compounds, cholesterol, some reducable sugars and finally hemaglobin and often oxyhemaglobin.

Here and there appear in the body cavity, connected to various organs and invading interstititial spaces, small strand-like materials, which give one the impression of a loose connective tissue. This material was called by K. C. Schneider (1902) "Bindegewebe" and by Looss "strand-like organs." The former did not locate nuclei within the mass, while the latter has reported finding them in two places, and suggests an homology between these organs in *A. duodenale* and the phagocytic organs or "büschelförmigen" organs of other species. Goldschmidt (1906) has called this tissue "Isolationsgewebe" and in the large ascarids has located a few cells in this structure situated just posterior to the nerve ring. I have been unable to find nuclei in this issue in *C. americanus* but this is not surprising, since one would expect them to be very minute and might easily be overlooked. No function nor homology can be proposed at the present time for this structure in our species, and the literature on the subject, tho large, is very much confused; that the whole problem will have to be worked over carefully before a conclusion can be reached is evident; the larger forms will have to be examined first before the smaller ones are studied. I am under the impression

that authors have been dealing with the same structures here and that it will prove to be nothing more nor less than a structure similar to the mesentaries and supporting ligaments of other animals, for holding in place the various internal organs. If this be true the name proposed by Schneider is much better than that given by Goldschmidt. Looss' name is at best a make-shift as would be any that I could propose.

The Reproductive Organs

Female. The female reproductive organs (Textfig. G) are of espe-



Textfigure G. Diagram showing the general arrangement of the reproductive system of the female. *ant.u.*, anterior uterine branch; *o.d.*, oviduct; *o. v.* ovary; *post. u.*, posterior uterine branch; *s.*, sphincter; *tr.*, trompe; *v.*, vestibule.

cial interest on account of the absence of the posterior ovary, altho its uterine branch is found. This is all the more interesting because in the Trichosyringata, an order not greatly removed from the Camallanidae, there is only one ovary found.

On superficial examination one might be lead to think that the posterior horn of the uterus was in reality a result of the mere mechanical lengthening of a single uterus, due to the enormous number of embryos developing within; but this is not the case, since in the very young females in which the ovary has not yet begun to function, this posterior branch is seen long before the female has been fertilized. At this stage it is merely a posterior thread of cells leading from the ovijector, corresponding to a similar anterior fundement. The details will be found elsewhere in the paper.

In the anterior division of the reproductive organs can be found, in general, the regions which have been found in most nematode species. There is distinguished an ovary, oviduct, with a "receptaculum seminis," and anterior branch of the uterus.

The ovary is pyriform in shape, attenuated anteriorly and ending in a rather long, slender cylindrical tube. Figure 66 shows the shape and the fact that the tube is about half the total length of the ovary. At the widest place the ovary is about 0.15 mm. The cylindrical tube increases gradually from 10 μ to 20 μ in diameter. Within this tube are recognized two areas as in the case of Ascaris and referred to by K. C. Schneider as the "Keimzone" and "Wachstumszone," each composing about half the length of the tube. In the former zone occurs an unorganized mass of primitive germ cells which begin in the posterior part of this zone to arrange themselves around the inner margin of the wall (Fig. 74). These cells are spherical in shape, 5 μ in diameter and with relatively large nuclei. Division of the cells takes place within this zone for here mitotic figures can be seen.

By growth, these cells come to fill the cavity of the tube so that only one layer around is seen and thus in the center they fuse (?) with each other, their peripheral ends being free. So is formed the characteristic structure found in most, if not all, nematodes (Fig. 73). The ovogonia appear like the spokes of a wheel, fastened by their fused ends, called a "rachis." In this species there is but a single rachis and about five or six ovogonia in each cross section. Under the force of this mechanical pressure they are compelled to assume

a cone shape but still have relatively large nuclei. This zone extends well down into the enlargement of the posterior region of the ovary where the last zone begins, the so-called "Reifungszone," where the cells begin to break away from the rachis and gradually assume a spherical shape again. In this region the first polar body is begun to be formed altho the process may be continued thruout the passage of the eggs into the oviduct. On leaving the ovary the eggs are about 25 μ in diameter with very large neuclei and prominent nucleoli, one in each nucleus.

There is nothing especially interesting about the histological structure of the ovary. A rather thick deeply staining basal membrane exists, and the wall is composed of a single layer of cells, very much flattened out and like typical pavement epithelial cells, with medium sized nuclei. As many as eight or ten cells can be seen in a cross section. As the ovary lies in the body, it is more or less coiled, but never more than twice, and these are very loose coils.

Posteriorly the ovary is rather sharply delimited by the appearance of a second layer of cells on the outside of the epithelial layer. These are cells with their inner sides muscular and a sarcoplasmic portion towards the periphery, giving the oviduct an irregular outline in cross section (Fig. 76). The nuclei of the muscle cells are in the sarcoplasmic portion. This layer of cells furnishes the oviduct with a circular layer of muscle and by peristaltic motion the eggs are shoved along. Coincident with the appearance of the muscular layer, the epithelial one becomes much higher so that the cells stick out more all around the wall into the lumen and here and there very large projections are seen, especially in one region, which I have designated as the receptaculum seminis.

In fairly mature worms, three regions of the oviduct are distinquished (Fig. 66); the first, about one-third the total length of the organ in 30 μ in diameter, then follows a second third, which suddenly expands to a diameter of 130 μ and contains shortly after copulation a mass of spermatozoa; few are to be found elsewhere in the system. Here the projections into the lumen (Figs. 75, 78) are very much larger than elsewhere, and groups of spermatozoa can be seen clinging around such out-jutting pieces. Fertilization (Fig. 68) takes place here or perhaps in the very anterior region of the uterus. Posteriorly this receptaculum seminis reduces in diameter to about 17 μ and the

musculature becomes very much thinner, until it disappears at the anterior margin of the uterus (Fig. 66). The epithelial cells remain high thruout its entire course and no valves are encountered in this region.

It is interesting to note in passing, that in cross section of the receptaculum seminis the spermatozoa are cut transversely as well, showing that their orientation is with the long axis of the uterus and oviduct; they apparently progress up the entire length of the uterus and posterior third of the oviduct, head first, maturing as they travel, to waylay the egg cells as they pass thru the oviduct. The fluid of the uterus and oviduct offer a medium for their progress.

Five worms were used for the compilation of the following table. The reproductive organs were carefully dissected out and preserved, stained and measured in xylol before they were sectioned. Unfortunately the total length of the worms could not be gotten since the dissections had to be made while the animals were still alive and they were so active that it was impossible to ascertain their lengths at that time.

A study of the sections showed that the shortest ovary and oviduct belonged to the youngest worm, and that they then arranged themselves according to the table, with the fifth as the oldest female. It becomes obvious that both the ovary and the oviduct grow with the worm, but that there is a tendency for the ovary to outgrow the oviduct, an altogether logical condition. Altho there are few cases given here it is perhaps a fair sample since they were picked at random from among a great many individuals.

III. OVARY AND OVIDUCT MEASUREMENTS

Organ	a	b	c	d	e
Ovary	1.9	2.0	2.4	3.2	3.5
Oviduct	2.0	2.1	2.5	2.6	2.7
Total	3.9	4.1	4.9	5.8	6.2
Ovary: oviduct	1:1.0	1:1.0	1:1.0	1:0.8	1:08

This uterus is simply a huge sac in which are contained the developing eggs and embryos, for this species is viviparous. Its walls consist of a single layer of pavement epithelial cells with fairly large nuclei (Figs. 64, 71) and cell walls more or less indistinct, the

basal membrane which is present stains deeply. There are no muscular fibers in the walls of this uterus, altho Cobb as well as other authors have described such in some nematodes. Looss failed to find them in *A. duodenale*. Within the uterus is a fluid which has been mentioned and this is precipitated by the killing and fixing fluids, stains well and is undoubtedly nourishing for the growing embryos (Fauré-Fremiet).

The anterior uterine branch is considered as beginning posteriorly at the inner end of the ovijector and continuing to the beginning of the oviduct (Fig. 65). The posterior branch ends blindly in a cul-de-sac (Fig. 67), and takes its origin at the common juncture of the two uterine branches and the vagina. Needless to say the uterus grows, probably by stretching as it becomes filled with embryos.

In living animals the uterus passes to and fro (antero-posteriorly) in the body cavity, undoubtedly due to the hydrostatic pressure within the body and the uterus itself, for the uterus lies free in the body, with no muscular fibers attached to it, being held somewhat in place by the before mentioned strands of tissue.

Adopting the recent terms of Looss and Seurat (1912, 1914) for the specific regions of the tube which leads out from the uterus to the genital aperture, I shall refer to this as the ovijector, for the sake of simplicity (Fig. 62). Taking up its structure from within outwards, it begins at the uterus as a tube 18 μ in diameter, posterior to the level of the vulva, being then directed anteriad at a sharp angle and lying at its origin on the ventral side of the body. Its course is by no means straight and its length varies from 1.3 mm. to 2.1 mm. It usually bends from side to side and in one female made a loose loop. Its angle is rather sharp where it starts towards the vulva.

The ovijector is lined thruout its course, save for a short distance at either end, with four rows of epithelial cells (Figs. 61, 72). These cells are rather unique in shape, being more or less round as seen in cross section and spindle-shape longitudinally (Figs. 21, 59). Their nuclei are in about the same level, so that in a given transverse section one sees four nuclei. These cells do not fill the entire cavity and a space extends between the four rows. The cells are 42 μ long. At the inner end of the ovijector the rows become a little irregular and not well marked out because of the appearance of more cells, so that it passes into the uterus without a valve and presenting no radical

histological difference. The covering of the tube is composed of a very heavy layer of circular muscles, which is anteriorly 10 μ thick and gradually dimishes in thickness until none can be seen at the exact juncture with the uterus. Many nuclei occur within this layer and the muscles obviously act as do those of the oviduct; by peristaltic motion they help to pass the embryos to the genital opening.

From a region just where the ovijector begins to turn towards the ventral side to its openings, this tube has a cuticular lining, which seems to be continuous with the external cuticula (Fig. 63). During the short distance in which the sphincter lies in the body cavity, there is around the cuticular lining a very heavy layer of circular fibers (Figs. 58, 62), with many nuclei, and which clearly function as a sphincter, their sarcoplasmic portions being towards the periphery. Sometimes the cuticular lining extends posteriorly over the four rows of cells, but then only for a short distance, and these cells do not appear very far forward of the end of the cuticular lining.

Thus the ovijector extends anteriorly past the level of the genital opening and suddenly makes a very sharp turn within the anterior vulvar lip, loses its musculature and passes posteriorly to open near the mid-ventral line of the body, but in the side of the vulvar lip towards the tail. This final tube (Fig. 63) is the "vestibule" of Seurat and is only a few micra in diameter and will allow of the passage of only one embryo at a time.

Just at the highest point of the turn a very interesting cuticular structure is present, which from its position and structure is considered as a valve, opening by its own elasticity and closed by the action of the sphincter (Figs. 58, 60). This valve is nothing more nor less than two, somewhat spherical, masses of material, apparently derived from and attached to the inner lining as tho they were mere thickening in its wall, and occupying a right and left position. Compression by the sphincter would push these two bodies together and thus close the passage way. There is the further possibility that they serve in some way during the act of copulation, e.g., in holding the spiculum within the vulva.

The vulva is very conspicuous in this species and is provided on both sides with a very prominent lip, of which the anterior one is the greater developed (Figs. 5, 58, 63). The posterior lip increases as the worms grow older so that in females just before giving birth

to embryos this lip is rather large and becomes pushed out to one side or the other by the overhanging anterior projection.

The anterior lip is about 0.3 mm. long and juts out about 0.12 mm. ventrally from the body; the shape is difficult to describe but can be easily seen in the figures as a swelled out portion of the ventral wall, overhanging its own posterior limit on the body wall.

In sections of the vulva one can see that the ventral band spreads out over the inner margin of the cuticula, and is very much thickened in the whole general region (Fig. 62); it becomes divided around the actual opening of the vestibule, which seems to pierce it, then unites below the opening to continue posteriorly as a single line or band. The cuticula is transversely ridged on the inner side so that it presents eleven definite places for muscle insertion (Figs. 5, 63).

Special muscles exist in this region, there being twelve large cells, each with a nucleus and having its greater insertion on the cuticula, then converging, they find their second insertion around the end of the sphincter and vestibule. Thus one sees in longitudinal sections a radiating structure of muscle cells in this region.

Contraction of these muscles will pull up the lower overlapping portion of the vulvar projection and at the same time turn the opening away from the body wall, while the elasticity of the wall itself will tend to restore it to its original position, aided by the contraction of the muscles in the lower portion of the vulva. These muscles are evidently modified somatic muscle cells. Their function, while possibly related to the expulsion of the embryos, is most likely involved in the act of copulation as well.

Larvae. It does not lie within the scope of this paper to discuss in detail the larval stage of this parasite, however, a few words will not be amiss. The larvae appear within the uterus of the female in two conditions, but in the first stage only. The two conditions referred to are (a) a phase in which the first cuticula is closely applied to the body and is the youngest phase, and (b) a phase in which the first skin is loose and the larvae are contained within it. When the larvae are freed from the female they are very active and the first skin is shed within a few hours, they then being in the second stage.

In the uterus these larvae are at times very active and can be stained in vitro with methylene blue. Those in the first phase stain

readily but those with the two skins do not stain until after several hours. They range in length from 200 μ to about 360 μ, and occasionally they are found as long as 540 μ, but this is unusual. Several regions can be located, in particular an anterior region, which has a great many nuclei and is about one-third the total length of the body. This is evidently the start of the esophagus. A light staining area passes around this regions and is interpreted as being the beginning of the nerve ring.

In cross section the larvae are seen to be made up of a tube of cells, about nine appearing in such a section (Figs. 121, 122). The anterior end is bluntly rounded off, while the posterior tip is sharply pointed (Fig. 10). Even in young individuals there are four nuclei in the anterior tip (Fig. 11) which stain deeply and are more distinct than any others in that region. Perhaps they are the foundation of the complicated subcuticular head structure and will form the oral apparatus. On the whole the nuclei of the body are very numerous. and occasionally one or two can be seen inside the tube of cells of which the worms are composed.

Some attempts have been made to find the life history of this species, but so far they have led to negative results. The larvae will live in water for several weeks, but they grow little and do not moult after the first skin has been cast, so far as was learned. These young stages are not as a rule in the intestine of the host. Every thing points to the necessity of an intermediate host in this parasite as in the case of *Camallanus lacustris.*

Male. The reproductive organs in the male nematodes are characterized by their simplicity and in this respect *C. americanus* does not differ from the general type, altho some peculiarities exist. There are three regions in the reproductive organs proper (Textfig. H), all within a single tube on the ventral side of the body, which may be displaced to the right or left, or parts of the tube may occur on the dorsal side in old animals where the tube has become long and sinuous.

The anterior region is known as the testis. This varies in length in different individuals according to their ages. In the young it is almost straight, in older forms it may have several bends, a loop, or may turn back on itself in the esophageal region and grow posteriorly almost to the anus. This tube is at its extremity 10 μ in diameter

and, after about 130 μ, has usually a small enlargement about 20 μ x 30 μ (Fig. 101). Then the tube very gradually enlarges up to a diameter of 35 μ, passing without much differentiation into the seminal vesicle, which, at its anterior end is about 65 μ enlarging up to 130 μ at its widest place in the posterior region. This part of the

Textfigure H. Diagram showing the general arrangement of the reproductive system of the male. *de.*, ductus ejaculatorius; *s.v.*, seminal vesicle; *t.*, testis.

system is about 3.3 mm. long. It passes into a small short tube and then into a region known as the ductus ejaculatorius continuing to the cloaca into which it empties on the ventral side (Fig. 92). This latter organ is about 2.2 mm. long and has an anterior diameter of 66 μ, narrowing to 20 μ just before the cloaca and to about 10 μ at its entrance into the common posterior ending of the genital and alimentary ducts.

In toto mounts these regions are well marked by their differences in staining. Of the three, the last region stains the deepest, the testis next and the seminal vesicle very lightly.

The spicula should be mentioned here as being accessory genital organs.

There is nothing especially interesting about the testis which has not been previously considered by zoologists. It consists of a tube, made up of a single row of cells with small nuclei, rather hard to find and comparatively few in number. The cells are very much flattened out and have a rather heavy outer basal membrane (Fig. 83). In the very anterior end of the testis, which ends blindly, are found the primordial germ cells and these can be seen, as in the case of the ovary, as very small cells which divide rapidly, as seen by the frequent mitotic figures. Further down in the testis the rachis formation is noted.

The seminal vesicle is but an enlarged portion of the system and contains in mature forms a great mass of germinal cells, before copulation has taken place. The cells here are free from the rachis. The walls of this region (Figs. 80, 104) are in direct continuation with those of the testis and but for an external constriction there is not a sharp delimiting area. The cells are more spread out here so that they become very narrow and with small nuclei. The size of this region is determined chiefly by the amount of germinal products present.

These products are considered by most authors as still being immature until after they have been for sometime in the uterus of the female. Looss, however, speaks of "mature spermatozoa" in this region of the system in *A. duodenale* and refers to a "mantle" surrounding nematode spermatozoa (1905:111). Concepts differ from other evidence and I am at a loss to explain his observations. The passage of the seminal vesicle into the last region of the system is indicated by the appearance of high epithelial cells and an outer muscular layer. The epithelial cells crowd in at the anterior end and thus form a kind of valve (Fig. 112).

The ductus ejaculatorius of the male reproductive system (Figs. 81, 97) is composed of two layers, the outer of which, consists of a circular musculature containing a very few nuclei, which appear in the sarcoplasmic part, and project out a little on either side of

the tube. This muscle layer is thin and must act as a muscle to produce peristaltic motion, functioning in the removal of the spermatic fluid from the male generative organs.

The inner layer of this tube is cellular and composed of rather tall columnar epithelial cells, about twelve being seen in a transverse section. These cells are extremely granular and have moderately sized nuclei. Figure 81 shows a cross section of this organ. . Reproductive cells are sometimes seen in this region but when crowded down by the formation of the products in the tube above, and hence only in the older specimens.

For the function of the epithelial cells I can offer but one suggestion, they may secrete, at the time of copulation, a fluid, perhaps gelatinous, which accompanies the sperm into the uterus of the female. This fluid may be nutritive or may be merely a mechanical carrier for the cells. I have sought in vain for information which would lead me to believe that this organ secretes a cement to stick the male to the female during copulation. The fact that the male cells are not generally retained in the ductus ejaculatorius for a very long time, presents some difficulty for considering it as secreting a nutritive fluid, yet after they have gotten into the uterus of the female there is yet necessity for some nutrition of the developing spermatids. It would seem as tho some fluid medium was necessary for conveying the male cells into the female and it seems most logical to believe that this organ secretes such a fluid.

The statements of Looss concerning this organ in the hookworm are not easily followed for he has included the description of the cement glands in the same chapter, but one is led to believe that he did not see a muscular layer around the organ; such a layer certainly exists in our species and has been noted in many other forms as well.

A further word concerning the spermatic cells. They reach maturity in the seminal recepticle of the female and there as has already been noted they may be seen oriented with their long axis parallel with that of the uterus and oviduct. They apparently have, their "heads" pointing anteriorly. Their shape is of interest; they are elongated and about 16 μ; have a short pointed tail and three more or less deeply staining areas, about equal in size and bulging out somewhat (Fig. 82). They are 3 μ wide in the widest place.

The spicula present a rather characteristic appearance in this species. The right one (Fig. 94) is by far larger than the left and differs in some other respects. The smaller (Fig. 95) of the two is but slightly curved and has no embellishments of any nature, being slender, acuminous in form and tapering from a diameter of 8 μ to a very fine point. Its total length is about 310 μ in all specimens, and ends anteriorly in an acute angle.

The right spicula is 18 μ in diameter anteriorly and it also has an acute angular anterior ending, so that a cross section near its anterior end shows only a crescent-shaped structure (Fig. 90). This speculum is about 870 μ long and is also acuminate in form. It is slightly curved and 75 μ from its tapering point has on its dorsal side a small point (Fig. 93) projecting dorsad and 5 μ long, curving slightly anteriad. Posterior to this point the spiculum dips sharply ventrad and then rapidly tapers to a fine point.

The structure of the spicula is very interestin and has been given in detail by Looss with whom I agree in the fundamental points. They consist of tubes (Fig. 88) of cuticular material, which dissolve in concentrated alkalis and stain deeply with almost all stains. The shell of the right spiculum is 4 μ thick and about eight times as thick as the smaller one (Fig. 89). Near their posterior tips they become solid. The cavity is filled with a very granular "pulp" which contains nuclei at the anterior end only. Sections show that this pulp is continuous with the outer covering of the spiculum (Figs. 90, 103), which is called the "spicular sheath" or the musculi exsertores spiculorum. In this mass of tissue which appears just at the head of each spiculum are from three to five small nuclei, evidently the nuclei of this tissue, although others will be mentioned later.

The extensor muscles are essentially alike those described for other species. In *C. americanus* this muscle (Fig. 96) is about 5 μ thick in the case of the large spiculum and 2 μ in the smaller, the thickness varying a little with the degree of contraction of the muscle. It seems to present two distinct layers of which the outer is a little wider and more granular, corresponding to a sarcoplasmic layer, and in this layer from time to time are noted large spherical nuclei (Fig. 103), especially near the posterior end of the organ. The inner layer is differentiated into fibers and is evidently the contractile layer of the muscles. Because of its intimate connection with the heads of the

spicula and its lack of attachment along their courses, its acts like a spring to shoot the spicula out when they are to be protruded. For this purpose they have been anchored firmly at their posterior ends and this is provided for by the places of insertion (Fig. 103) on the dorsal wall of the cloaca in a manner to be described a little later.

Other muscles have yet to be mentioned in connection with the spicular apparatus; these are the musculi retractores. They are seen in single masses of fibrous tissue attached to the heads of each spiculum (Fig. 103) and extending for a short distance underneath the spicular sheath. On the oblique side of the anterior end of the spiculum this mass sends out several small branches which become attached to the spiculum and somewhat embedded in its pulp (Fig. 86). In each case the single mass divides a short distance anteriorly into two long slender muscles, which proceed, two on either side of the body, free in the body cavity, (Fig. 97) for a distance of about one-fourth the total length of the body to their respective anterior insertions. Each muscle has about half way in its course a small amount of sarcoplasm surrounding a nucleus (Fig. 105). The muscles of the left spiculum are correspondingly smaller than those of the right and are not quite so long. After the muscles have divided, they pass anteriorly, each member of a pair running close together and become inserted at each of the four sides of the lateral lines.

The spicular canal (Fig. 100) has been discussed at length by Looss and to his account I have little to add. The structure has been called by some authors the "spicular sheath" but as Looss clearly points out, it is a separate structure, and should therefore be given another name.

The canal appears on the dorsal side of the cloaca where two very small cuticular wings arise on either side of a small groove, which has a cuticular lining. The lining is covered with a granular layer of protoplasm which contains a few nuclei, three according to Looss. This single canal continues anteriorly at a sharp angle from the cloaca and shortly divides into two grooves into which the spicula project, their sheaths being firmly inserted on this structure; the cuticular lined canals continue but a short distance anteriorly.

The Nervous System.

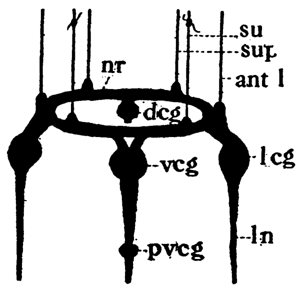
Comparatively few points are known and understood concerning the morphology of the nervous system of the nematodes as a

whole. The enormous mass of literature that has accumulated on the subject has concerned itself with the nervous system of *Ascaris megalocephala* and *A. lumbricoides* and while it has contributed to the morphology of these systems, it has chiefly been concerned with the various problems in the neurone theory, cell constancy, etc., offering considerable information on these subjects. In addition to this, these workers (Apáthy 1908; Goldschmidt 1907, 1908, 1908a, 1909, 1910; Deineka 1908, 1912) have investigated the members of the genus Ascaris admittedly the highest specialized of the group, and many conditions are found in this genus and in particular these two species which appear in other nematodes in a much simpler and more elementary stage or are totally lacking.

It does not lie within the field of the present paper to consider these problems and no attempt has been made to present a review of the literature which has been so well done by de Rouville (1910, 1911). The work of Looss (1905), because of its strictly morphological character, will demand consideration and since it is really the only piece of work that is at all complete, reference will constantly be made to it.

One is struck in looking over this work with the apparent ease with which Looss was able to trace out the minute fibers and locate the most delicate connections and for all of this he gives no special technique; one must conclude that he did the work on material preserved in glycerol-alcohol and handled according to his method which is at best poor for working out the finer details. One cannot help but marvel when he reads of nerves which "are small and may consist at most of two or three fibers," or "the first fiber which leaves the ganglion," etc. Every method known has been tried to demonstrate the nervous system in *C. americanus* and it is only after many trials and piecing out gaps in each method that the conclusions about to be set forth have been obtained, which I regret to say are all too fragmentary and liable to error. If the finer connections, comparable to those described by Looss in *A. duodenale* really exist in my species, I have failed to locate them and have difficulty in believing that they are present in one species and not in the other, altho one is not surprised at even greater differences between *C. americanus* and the genus Ascaris. In one or two of the major connections are to be noted differences in my species and Looss' description.

Like most nematodes, there exists in this species a nerve ring, better referred to as the *cephalic commissure.* There are associated with this commissure twenty cells in each lateral half, in all forty cells, of which some may be adventitious, and the greater number are just anterior to the nerve ring. The rest are just below it, altho some are scattered in the subcuticula surrounding the esophagus. Some of these cells anterior to the nerve ring are found in groups in definite places. From these groups six nerves pass anteriad, while two are laterals, two sub-dorsals and two sub-laterals. (See Textfig. I for diagram of the nervous system). A further word will dispose of



Textfigure I. Diagram of the cephalic part of the nervous system. *ant.l.*, *d.c.g.*, dorsal cervical ganglion; *l.c.g.*, lateral cephalic ganglion; *sub.l.*, anterior sub-lateral nerve; *sup.l.*, anterior supra-lateral nerve; *v.c.g.*, ventral cervical ganglion, *n.r.*, nerve ring; *p.v.c.g.*,postventral cephalic ganglion.

these nerves; they supply the region anterior to the nerve ring, and each runs forward very close to the esophagus and supported by surrounding subcuticula. The two sub-ventrals have within their course near the anterior tip one nerve cell in each (Fig. 14), and these give out branches to supply the adjacent tissue. Nerves in Ascaris and Ancylostoma are found passing anteriorly also, but these go to papillae, none of which exist in *C. americanus* so that I refrain from homologizing these structures until more is known about them. Under the present condition I believe that the nomenclature for these nerves should be based upon their position alone.

Below the nerve ring one can recognize five ganglia which are called the dorsal cephalic ganglion, the ventral cephalic ganglion, the post-ventral ganglion and the two lateral ganglia. Commissures

connect the latter two with the nerve ring on the one hand and the ventral cephalic ganglion on the other. Longitudinal nerves arise from each ganglion.

As has been clearly pointed out by previous authors, the cephalic commissure, or nerve ring, is composed essentially of fibers which originate from the ganglia, hence this structure is not regarded as the fundamental part of the nervous system. In *C. americanus* the nerve ring (Figs. 3, 34, 52) is in direct contact with the esophagus all the way round and is contributed to by tissue from all four longitudinal lines, altho Looss maintains that the dorsal one plays no part in this formation in the hookworm. The fibers themselves are chiefly, if not entirely, from the ventral and lateral cephalic ganglia. The nerve ring is slightly oval in cross section and about 10 μ in diameter. The fibers are supported by loose tissue network of subcuticula origin.

The dorsal cephalic ganglion is the smallest of the anterior ganglia (Fig. 54) and is situated on the inner side of the dorsal longitudinal band just beneath the nerve ring. It consists of but three small cells which give rise to the dorsal nerve, which in turn continues posteriorly in the dorsal line.

The ventral cephalic ganglion is horse-shoe-shaped (Figs. 52, 54) and lies at a little more posterior level than the dorsal cephalic ganglion. From it pass two large masses of fibers to the nerve ring (Fig. 53), and posteriorly the collected fibers from the ganglion pass towards the tail in the ventral line. This ganglion consists of about twenty-five cells of varying sizes, each having a relatively large nucleus with a single nucleolus. Further, from this ganglion pass a right and a left commissure in the subcuticula to reach the two lateral cephalic ganglia.

The post-ventral cephalic ganglion appears a short distance posterior to the ventral cephalic ganglion and in the course of the ventral nerve (Fig. 55). As a matter of fact it appears at the opening of the excretory duct, lying immediately above it, and is composed of three or four small cells. Goldschmidt has described a similar ganglion within the course of the ventral nerve in Ascaris and these two are probably homologus.

The lateral cephalic ganglia (Figs. 35, 54) are by far the largest of the ganglia and are directly connected to the nerve ring, altho Looss failed to find such connections in *A. duodenale*. These ganglia begin

on about the level of the ring and gradually increase in size, occupying the inner margins of the lateral lines, even dipping in between their two halves. Posteriorly, they diminish in size until a few cells string out nearly to the level of the cervical papillae. The commissure to the ventral cephalic ganglion has already been mentioned. A nerve goes from each ganglion to the cephalic papillae on the same side and posteriorly the lateral nerves arise. I can be certain of only one on each side, and these continue caudad in the lateral lines, in the anterior region of the body, near the cuticula and in the mid-lateral line. There are about thirty cells in each ganglion.

At the hands of both Apáthy and Goldschmidt, the minute structure of the ganglionic cells in Ascaris have received special attention, and these authors have offered many interesting considerations, most of which involve physiological inferences and explanations which lie outside the present work. In brief, Goldschmidt has found that typically three zones exist in the ganglionic cells, an outer, middle and inner. The outer zone is made up of a rather coarse alveolar structure and borders the cell. The middle layer has smaller alveoli and is continuous with the nerve process. The inner zone, also alveolar in structure, lies immediately around the nucleus. Various modifications occur in the various cells of the ganglia so that in most of the bipolar cells one fails to recognize separate zones. Furthermore, one often notes that the borders of the alveoli are so arranged as to give the cell the appearance of being made up of radiating structures, and again this latter type of cell may be further modified to present a "central body" around the nucleus, which is continuous with the neurofibrills. Fibroid substance is present in varying amounts in all the cells.

While so complete a study of the histology of the nerve cells in *C. americanus* has not been made as Goldschmidt has done in the case of Ascaris, I have nevertheless satisfied myself that the conditions here, while essentially like those in this genus are not so complicated. These cells are small, the largest having a short axis of about 30 μ and the structure is therefore hard to make out. In only a few instances could neurofibrills be recognized, but in good preparations one can see and follow for some distance the nerve processes of the cells. Figures 106 to 109 show several cells drawn from one of the lateral ganglia. In none of these cells have I been able to recognize

three distinct zones altho there is usually a thickened area around the nucleus. Figure 108 shows a central body and distinctly radiating protoplasm and the nerve fiber continuous with the central body, exactly as Goldschmidt has figured it for Ascaris. The other cells show beautiful alveolar structure but zones are not marked off. In the bipolar cells the alveoli are very small.

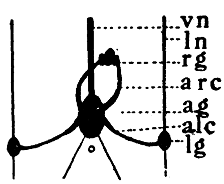
Within the cephalic ganglia has been noted only two types of cells, agreeing with Goldschmidt's unipolar and bipolar types. Perhaps multipolar cells exist also, but these have not been seen.

The longitudinal nerves are extremely difficult to trace thruout their courses and I cannot give a positive statement of their behavior except in certain regions. The dorsal nerve continues to the tail in the dorsal longitudinal line, supplies the somatic muscles with nerves and diminishes to an uneventful ending near the posterior end of the body.

The ventral nerve is the largest of all and can be found in the ventral line (Figs. 53, 119). This nerve also supplies the muscles of the body and in the posterior region enlarges greatly. Its ultimate fate will be considered in a special section.

I am not at all sure of the lateral longitudinal nerves, they are small and arise at the base of the lateral cephalic ganglia. Each gives a branch to its corresponding cervical papilla (Fig. 111) and continues posteriorly in the lateral lines. One cannot say whether these nerves are doubled or single thruout their courses. They become involved in the complicated structure of the caudal end of the body, which is so different in the two sexes as to demand separate consideration.

In the female as the ventral and lateral nerves approach the tail they become much thicker and here there is only one lateral nerve in each lateral line, carried near the excretory canal and taking its place in position when the excretory canal ends. (See textfigure J).

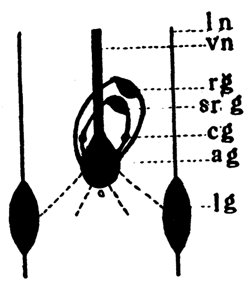


Textfigure J. Diagram of the caudal part of the nervous system of the female *a.g.*, anal ganglion; *a.l.c.*, anolumbar commissure; *a.r.c.*, anorectal commissure; *l.g*, lumbar ganglion; *l.n.*, lateral nerve; *r.g.*, rectal ganglion; *v.n.*, ventral nerve.

Just anterior to the anus a ganglion appears in the ventral nerve and contains from four to five cells (Fig. 130). A relatively large commissure passes on either side from this, the anal ganglion, around the rectum to join with the rectal ganglion which lies on the dorsal side of the rectum a little anterior to the anal ganglion. This rectal ganglion has only three cells in it, a large medin one and two smaller laterals.

There are right and left ganglia in each lateral nerve called the lumbar ganglia, each consisting of five or six cells and these lie a little posteriorly to the level of the anus on the inside margins of the lateral lines. A small commissure connects the lumbar with the anal ganglion. Nerves continue into the tail from each lumbar ganglion and two small nerves pass posteriorly from the anal ganglion, one on either side of the anus.

It will be noted that the caudal nervous system of the male very closely corresponds to the condition in *A. duodenale*, the most important difference, which is of no consequence, being that in the hookworm there is a paired anal ganglion; in this respect it differs from the condition found in Ascaris and *C. americanus* (Textfig. K). The



Textfigure K. Diagram of the caudal part of the nervous system of the male. *a.g.*, anal ganglion; *c.g.*, cloacal ganglion; *l.g.*, lumbar ganglion; *l.n.*, lateral nerve; *r.g.*, rectal ganglion; *sr.g.*, sub-rectal gland; *v.n.*, ventral nerve.

same statement might hold true in the case of the female as well. One other difference will be pointed out later on as regards the males.

While differences occur in the two sexes in respect to the nervous system in the caudal region of the body, they can still be homologized in most instances, if not entirely.

The ventral nerve becomes very much enlarged at the beginning of the region of differentiation in the caudal end of the body of the somatic muscles (Fig. 87) and here and there, branches from these caudal muscles bend over to the ventral nerve for their innervation. Just anterior to the ano-genital aperture there is found the anal ganglion (Fig. 92). In the males as in the females this ganglion is not paired, but in the former it is very much larger, for it contains about twice as many nuclei. From this ganglion I have been unable to trace nerves but two commissures were found. These arise very close together and pass dorsally (Fig. 99) and at the same time anteriorly, one of them assuming a more anterior position than the other. This one goes to the rectal ganglion (Fig. 98) which lies on the dorsal side of the rectum in the same relative position as the rectal ganglion in the female.

As in *A. duodenale* this ganglion seems to have been divided for another small one is found posterior to it and between the spicular canal and the rectum (Fig. 98). To this ganglion, the sub-rectal, the second commissure from the anal ganglion passes. In its course are found ganglia lying on either side of the cloaca, for this commissure passes obliquely around the cloaca, and since corresponding cells in *A. duodenale* have been called by Looss, the cloacal ganglia, the name for the structure here described will be retained.

In the lateral lines, beginning a little above the anus are found ganglionic cells in the course of the lateral nerves. At first these are but a few cells, but on passing backwards, the number of cells in each lateral line becomes greatly increased (Fig. 84), until below the anus there is a considerable mass of ganglionic cells, which continue almost to the tip of the tail. Nerves from these ganglia supply the ribs of the caudal region of the male. I have tried to find one or more commissures to the anal ganglion, for they surely must exist, but so far the attempt has been unsuccessful, for the region is very hard to study on account of the condition of the tail in preserved specimens, it usually rolls in such a manner as to preclude the possibility of getting good sections.

Looss has noted in *A. duodenale* three pairs of lateral ganglia in this region and he has termed them beginning anteriorly, the lumbar, postlumbar and costal ganglia, but since in *C. americanus* there is no definite division of the ganglia, I propose to call this pair in this

species, the lumbar ganglia, believing them to be homologus with those in the female and possibly with all three pairs in the case of *A. duodenlae.*

Nothing of especial interest happens in the case of the dorsal nerve in the caudal region of the males.

While sensory endings are more varied and of greater frequency in the free-living nematodes, they are by no means lacking in the parasitic species. Unfortunately no detailed study has been made on the free-living forms and only in the genus Ascaris has a careful and more or less complete description been given of the sensory endings in parasitic nematodes.

By position there are three groups of sensory endings in most nematodes, altho one or more, or perhaps all may be lacking in special cases. Typically then, are found papillae with sensory endings in the head region, a pair in the "neck" region in a lateral position and finally papillae in the caudal region of the male. So far as known there are no nerve endings in the caudal papillae of the females when such structures occur, but no statement is found in literature which points to a careful study of this point.

It is out of the place to enter into the discussion between Goldschmidt and Deineka and I have little to offer in support or against either of the two authors. In *C. americanus* the structures are all very much simpler and almost totally unlike those in Ascaris; in addition to this, there is the unfortunate fact that the structures are so small as to preclude the kind of work done by these two authors mentioned above. Since there are no "head" papillae in *C. americanus* one can omit a discussion of their work on the papillae of the lips of Ascaris; a few words will indicate some of the points brought out by Goldschmidt, since his work is very complete and differs from that of Deineka only in interpretation and a few minute points of anatomy which being so different in *C. americanus* do not concern this paper.

The cervical papillae are found laterally in Ascaris and do not project out into the exterior. They are rounded masses of subcuticula which have pushed up into the cuticula. In the lateral line, connected with these papillae, are found two cells, the Stützzellen and the Geleitzelle; the former contains the nerve, which in this case, before its end, has an enlargement, then it has a deeply staining swelling

and finally a very dark staining "Trichterplatte" and an end body for the very terminal portion of the nerve. The neurofibrillae do not pierce the covering of the body, the entire structure of the papillae being below the surface and covered by the cuticula.

In the anal papillae one sees a different structure in the genus Ascaris. Here the cuticula is projected out into a more or less pointed papilla and at its periphery is a minute hole leading into a canula which is a part of the Stützzelle and contains the nerve. The sensory apparatus consists of from one to three nervefibers which are very simple. There is a chromatic portion of the nerve near its periphery which stains deeply. The Geleitzelle is lacking.

Looss mentions the innervation of the cervical papillae in *A. duodenale* but has studied the entire structure very little. He said that the pulp of the organ was of subcuticula and that its nerve supply was from the post-lateral cervical ganglia. No details of the nerve endings were given. The innervation of the few papillae in the male tail he stated to be from the posterior ganglia. No details of their structure were given either.

Strictly speaking there are no true papillae in the tail of the male but the structures usually referred to under that name are really ribs, if one considers a papilla as a formation from the entire cuticula, while a rib is covered, except at its tip, by only the lower layer or layers of the cuticula.

In *C. americanus* the cuticula divides into two layers at the beginning of the lateral alae (Fig. 87), and as has been mentioned previously, the tubes are short, cylindrical ribs (Figs. 79, 87) which occupy certain positions extending between the two layers. These are tubes covered over by the lower layer of cuticula from which they can be seen to arise in Figure 87. Into these tubes the subcuticula extends.

At the periphery of such a tube is a minute canula which extends down into the tube one micron and is evidently a product of the subcuticula. Over the peripheral end of the tube of the lower layer of the cuticula, there extends the outer layer, so that this end of the rib becomes enclosed in a cap of outer cuticula.

The nerve endings in the papillae are interesting. They consist in each case of two minute fibrillae which run in the subcuticula very close to the inner sides of the tube and terminate in two chromatic

portions (Fig. 91), spherical in shape and lying at the base of the little canal. If, as in the case of the anal papillae of Ascaris, minute fibers run into the canula from the chromatic portion, I have been unable to trace them. Special supporting and accompanying cells for these papillae could not be found but their innervation is from the posterior ganglia. In short they seem to be combined ribs and papillae. All of these ribs have the same kind of structure except that the postanals and paraanals are shorter and thicker (Fig. 79). Usually the peripheral end of the tube is slightly dilated, this condition being more marked in the post- than in the pre- anal papillae.

The cervical papillae are but very slightly raised above the general contour of the body and are not exactly lateral, they being slightly dorsal to the middle of each lateral line.

The *pulp* of the papillae lies well embedded in the cuticula and is in the shape of a little knob, not perfectly smooth in outline, but slightly bulging, so that in sections one sees little swollen sides of the knob (Figs. 102, 110, 111). This knob is composed of subcuticula. Here again I have been unable to locate the two cells found by Goldschmidt in connection with this organ in Ascaris.

The nerve supply is from the lateral nerve (Fig. 111), a branch coming off anterior to the papilla and then running into it as a moderate sized bundle of fibers. These fibers end peripherally in a deeply staining mass at the termination of the knob. Set into this structure thru a hole in the cuticul is a minute spine which has its inner end directly above the nerve ending.

Here it would seem that the whole structure is remarkably simple and its mechanism is easier conceived than in the case of Ascaris, for in *C. americanus* there is a spine to communicate the stimuli to the nerve endings, while in the case of Ascaris it is necessary to assume that the stimuli are transmitted to the nerve endings thru the direct effect on the cuticula itself.

In most free-living nematodes the so-called amphids are found in a somewhat similar position to the lateral cervical papillae in the parasitic species and it would be decidedly worth while to study these two structures in a comparative way to see if the two are homologous.

IV. YOUNG FEMALES

In the examination of turtles for *C. americanus* only twelve young individuals have been found. These are all females and are near the same age if the lengths of the bodies, thickness and conditions of the genital organs are indications of their ages.

They are about of the same proportions as the adults so far as the body size is concerned and each has already the three spines (Fig. 7) on the tip of the tail. The esophagus is divided into two regions and the "bridge cell" is present (Fig. 56). The intestine shows some pigment and the tail is about 0.1 mm. long. The ovijector can be seen near the middle of the body and from it stretch out, as two arms, the beginnings of the genital organs. The oral apparatus is present, light yellowish-brown in color and somewhat different from the adult, the details of which will be taken up later.

Seven individuals have been studied in regards to certain measurements which appear in Table IV.

It will be seen that these specimens range in length from 3.3 mm. to 4.7 mm. As they increase in length the diameter of the body also increases so that the smallest one has its greatest diameter 0.1 mm. which was taken a little anterior to the fundement of the ovijector, the longest worm is 0.14 mm. thick. It will be seen at once that the ratio between the length and the thickness is not exactly constant but very nearly so, which is not the case in the adults. In these young worms the ratio is about 1:33. It would seem therefore as if the mature worms grow longer faster than they grow wider, while in the young forms both dimensions grow alike. Undoubtedly the development of the embryos within the uterus accounts for the difference to a great extent, so in the males the development of the testis explains this, since elongation is probably more easily accomplished than enlargment in diameter.

The average of the lengths of the anterior region of the esophagus is 0.36 mm. which is not greatly below that of the adult females, while in two individuals this region of the esophagus is as long as in some adults. In other words this region is almost grown in individuals in which the oral apparatus is not yet completely formed and the reproductive organs are extremely immature.

The average length of the second region of the esophagus is also but little shorter than in the case of adults, but here again one finds

in certain individuals that this region is already as large as in some adults. The average length of these younger forms is 0.46 mm. That the esophagus develops early and to its maximum length is clearly shown in the case of this species.

While the lengths of the two regions of the esophagus compare very favorably with those of the adults, the thickness of this organ is less in the younger individuals as would be expected, since the body width is so much less. The greatest thickness of the anterior region of the esophagus in the younger forms is about 0.055 mm. while in the average of the adults it is about twice as great. The growth then comes in the diameter of the organ rather than its length. It would be interesting to know if there is a correlation between the two but the material at hand is not abundant enough to study this point.

Another very interesting ratio is that between the post- and prevulvar regions. It will be recalled that in the smallest females which were mature, the prevulvar region was longer than the postvulvar region. This is also true in the case of every one of the immature individuals, so that the ratio between the two regions is, in the worm 3.3 mm. long, 1:1.2 and this ratio diminishes with a fair degree of regularity, considering the few specimens, to a ratio of 1:1.13. The ratio between the two regions in the youngest mature female in 1:1.1 which is in series with the ratios of the immature specimens. This demonstrates that at first, even in the very young specimens the prevulvar region is greater in length and that as the female grows the postvulvar region outgrows the anterior portion of the worm. This seems to be due not merely to the presence of the growing embryos, but rather to the growth of other tissue as well, since the same thing is noted for the individuals without embryos.

Since the structure of most parts of these young forms is essentially like that of the adults and so much detail has been given for the latter, only those organs which differ greatly will be discussed here. Under the section on the cuticula of the adult, that of the young form has been treated so that there remains but to take up the oral apparatus and the genital organs; of these the latter will be considered first.

IV. MEASUREMENTS OF YOUNG FEMALES

No.	Body length	Body thickness	Length anterior portion esophagus	Length posterior portion esophagus	Length prevulvar region	Length postvulvar region	Ratio prevulvar: postvulvar lengths
1*	3.3	0.10	0.36	0.41	1.8	1.5	1:1.20
2*	3.5	0.10	0.34	0.46	1.9	1.6	1:1.18
3*	3.7	0.11	0.33	0.44	2.0	1.7	1:1.17
4	4.0	0.12	0.39	0.48	2.1	1.9	1:1.11
5	4.2	0.13	0.36	0.49	2.3	1.9	1:1.12
6	4.7	0.14	0.36	0.45	2.5	2.2	1:1.13
7*	4.7	0.14	0.40	0.50	2.5	2.2	1:1.13

*Without dorsal and ventral spikes (tridents?) on oral apparatus

Female reproductive organs. The reproductive organs are in the shape of the letter T with one arm bent over after a short distance and running back parallel to the cross bar. The T slants posteriorly (Fig. 9). The upright of the T is represented by a small cavity surrounded by cells, lined near its base with an extremely thin layer of cuticula. This portion (Figs. 69, 124) is the ovijector and in the longest forms at hand is about 70 μ and 25 μ wide. In the shorter specimens it is about as long as wide. There are as yet no projection of the cuticula in this region, so that the typical vulva does not exist, and there is no opening of the organ to the exterior.

In sections this ovijector shows that it is composed of two layers of cells (Fig. 69) just as the corresponding region of the adults, but the inner layer here has at first more than four nuclei in cross section, differing therein from the condition found in adults. Since by position this region is the vestibule and is later heavily lined with cuticula, the suggestion is here made that these cells in the younger specimens give rise to this lining. Mediad (Fig. 70) this condition changes so that there are but four cells seen in cross section as in the case of the adult and the circular musculature is quite well represented. This is the region of the vagina and "trompe," which passes into a very small tube of cells running off in two strings, one passing anteriad and the other posteriad.

These tubes do not have a muscular layer and the tubular condition is not very evident after a short distance (Fig. 85) for the tube is so small and the cells so large that they fill in the cavity. The nuclei are especially large as compared with the total size of the cells.

Posteriorly this string of cells continues to a little over half way between the vulva and the posterior tip of the body and must be the foundation of the posterior uterine branch. The branch which passes anteriad represents the future anterior uterine branch, the oviduct and the ovary. About 0.6 mm. from the vulva it makes a sudden turn and then runs posteriad to within a short distance of its origin. This condition was noted in every individual and leads me to believe that the region from the ovijector to the point of the turn is the foundation of the anterior uterus, for in the adult there always occurs a turn at the end of the uterus and the oviduct passes posteriad. The rest of the string of cells is a little thicker but with no differentiation in it. A muscular layer of the oviduct could not be found in this material.

The mouth apparatus. Altho some features of the oral apparatus as it exists in the young individuals have been considered earlier in the paper, there are other points which call for description here.

In general the same plan of construction is present in the young worms (Fig. 4) as in the older ones, but in the former the structures are much smaller and more delicate. Table V gives comparative figures for both.

V. MEASUREMENTS OF ORAL APPARATUS

PARTS MEASURED	YOUNG FEMALES	OLD FEMALES
Length	0.070 mm.	0.105 mm.
Width	0.080	0.160
Thickness outer layer	0.007	0.010
Thickness inner layer	0.004	0.005
Height of teeth	0.004	0.005
Diameter of the ring	0.050	0.100
Extension of ring below valves	0.030	0.017

The shape and structure of the lateral valves is almost identical with that of the adults. They are of a slightly lighter color but have as many longitudinal ridges as in the adults (Fig. 16). The two layers which have been mentioned before are demonstrable by staining reactions and these are slightly thinner than in the case of adults and the ridges are not quite so high. The two valves are united along their dorsal and ventral margins (Fig. 16, 19) and as in the case of the adults they are in contact with the cuticula.

The four giant cells are developed at this stage and apparently can function, for the worms are as tightly attached in proportion to their size to the mucosa of the host's intestine as are the adults.

The anterior wings (Fig. 15) are well developed but are smaller than in the adults and essentially like them. Whether the valves covers exist or not could not be ascertained from the material at hand.

Two striking differences exist in this young oral apparatus, the first of which is the condition of the ring. It will be noted by reference to the table that while the ring is only half so large in diameter, it is twice as broad as in the adults, that is, it extends further posteriorly from the margin of the valves. It must be remembered that the esophagus is narrower in these young forms and the appearance in the adults is as tho it had pushed out the margin of the ring when it expanded.

The second characteristic of this mouth apparatus is the absence of the tridents. In some of the individuals the dorsal and ventral margins of the valves are perfectly smooth while in others there projects out a small process from a point just below the union of their anterior margins. These projections vary in length in different specimens, the longest being 5 μ (Fig. 4). No indication of a cleft condition has been found and in all individuals they appear as single spikes. The significance of this will be discussed in the next section of the paper.

Discussion. From a study of the material at hand it is not wise to state positively the stage of the larvae which have just been described. However, the majority of facts indicate that they are, as yet, in the fourth stage, following the nomenclature of Maupas (1899). That is to say, they will moult again in the intestine of the host, just as do the hookworms.

There are some minor objections to this hypothesis; no indication has been seen in any of the individuals which suggests the preparation for the final moult. No deposits appear beneath the cuticula, and the coverings of these forms corresponds to the outer layer of the cuticula of the adults, as has been previously stated. Further, no indication of the formation of a second or final oral apparatus has been noted and the series of dorsal and ventral projections suggests the start of the tridents, which by further growth would develop into

the adult structure. Finally in no individuals found has anything been seen which would suggest a moult within the intestine of the host.

At the same time there is no positive proof that another moult will not take place. The failure to find intermediate stages is of course not sufficient ground for assuming that there will be no further development, and since the individuals are all so near the same condition of development, one would hardly expect to find different phases among them.

Up to the present time the most conclusive evidence for considering these forms as being in the fourth stage, is in the first place, the growth of the oral apparatus; in particular its growth in outside dimensions, is very difficult to explain. Before the form reaches maturity that organ will have to grow to twice the size it is in the young specimens. The second point in the evidence is found in the condition of the genital organs. The fact that no opening to the exterior has been found is very strong proof that this form is not yet in the fifth stage, especially since the vulva is absent and the ovijector is so extremely undeveloped. Until more material is found a conclusion on this point cannot be reached.

Considering all the information given in this paper on the morphology of the adults and the young, it becomes evident that this is a very important nematode species. In the first place this form is from a water host, and members of the genus Camallanus are found parasitic in host of three phyla. The hosts are from among the fishes batrachians and reptiles, all animals inhabiting water for the greater part of their lives, and species of this genus have been reported from both fresh- and salt-water hosts, in Europe, Africa and America.

In the next place this particular species is not only a member of the genus Camallanus but is in the great superfamily Spiruroidea, one of the most interesting and fundamental groups which exists. Upon the correct interpretation and description of its members will depend in a great measure the future knowledge of nematodes, especially from a systematic standpoint for this family clearly consists of a group of intermediate species. The divided condition of the esophagus and the two lateral lipped condition certainly constitutes one of the fundamental and important divisions of the Nematoda.

The nematode parasites of these water hosts as a rule show characters which more closely resemble the free-living species, than the parasites of the strictly land hosts, In this connection, a full discussion of the significance of the divided esophagus and the condition of the excretory system has been given in the paper and no further word is necessary here.

Again, the simplicity of the special endings of the nervous system indicates primative conditions. Not only are these endings in themselves very simple, but they are connected to the exterior while in Ascaris this is not the case. The rest of the nervous system, while complete in the essentials, is much simpler than in the case of the higher species of nematodes, as for example in Ascaris.

Not only does the condition of the excretory system and the function of the large cells in the esophagus suggest a relationship with the family Trichotrachelidae, which certainly are not very advanced above the free-living state, but the reproductive organs of the female are very much like those of this family. Even in the viviparousness of the family the genus Camallanus resembles it.

V. THE GENUS CAMALLANUS RAILLIET AND HENRY 1915

The name Camallanus was introduced by Railliet and Henry in 1915 as a designation for the genus Cucullanus of some recent previous authors which was not the original genus Cucullanus of Müller 1777.

Cucullanus was created by Müller to include two species, parasitic in the intestine of the cod, which he named *C. cirratus* and *C. muticus*, and later united in one species which he called *C. marinus*. Railliet and Henry have not considered these two names as referring to one species, thus they have come to select the species *cirratus*, because it was first named, as the type of the original genus. Dujardin (1845) gave the name of Dacnitis to certain members of the genus Cucullanus, but by the law of priority his name is no longer in good standing. Since members of this genus are distinct from those in the Cucullanus of Dujardin and subsequent authors, Railliet and Henry have given them a new name, that of Camallanus (*camallus*, a hood). The characters of this genus are stated by these authors as follows:

Camallanus Railliet and Henry 1915 (Cucullanus Auct., non Müller 1777). Polymyarians (Schneider), secernantes (Linstow). Cuticula finely transversely striated. Body usually red, obtuse anteriorly, more attenuated posteriorly. Head with two dorsoventral valves, limited by a mouth which is a transverse slit and an elliptical buccal capsule at its entrance; rounded behind, where the internal walls present longitudinal parallel ridges, usually terminating at the margin of the mouth in the form of small teeth. Behind this buccal capsule is a chitinous apparatus in the shape of two transverve bands united into a sort of band (apophysis Rud.); this part, on each side has a trident, diverging posteriorly, of which the lateral branches serve for the insertion of muscles to move the buccal valves. The valves are terminated by a circular "bourrelet" (pharynx Duj.) at its entrance into the esophagus. In general the esophagus is formed in two portions; the anterior muscular and clear, and the posterior glandular, more opaque and swollen.

Males with recurved and inrolled tails, carrying caudal alae which project a little and have a variable number of riblike papillae. A single spiculum, sometimes accompanied by a very small accessory piece.

Females larger, tails straight and conical, sometimes with two subterminal lateral papillae. Vulva projecting from the middle of the body. Viviparous.

In the development, an intermediate host functions.

Habitat: The adults live in the intestine or stomach of fishes, batrachians and reptiles. The larvae have been found in the body of crustaceans (Copepoda) or the larvae of aquatic insects, sometimes in the eyes of fishes.

Type *Cucullanus elegans* Zeder 1800 = *Echinorhynchus lacustris* Zoega 1776.

From the very careful study made of *Camallanus americanus*, another species of this genus sent from Africa by Seurat and placed at my disposal, and the two species, *Camallanus ancylodirus* and *Camallanus oxycephalus* described jointly with Professor Ward, the author is able to correct somewhat at length the generic description given by Railliet and Henry. The errors in their account are the following:

i. The valves are lateral and not dorso-ventral.

ii. The mouth apparatus is not a buccal capsule, but is composed of a pair of jaws, which indicate an origin from a lipped-condition.

iii. Two transverse bars, the so-called apophysis, do not exist.

iv. No muscles are inserted on the lateral branches of the trident.

v. The *bourrelet* is the esophageal cap.

vi. The second region of the esophagus is not glandular in the true sense of the word.

vii. There are two spicula in the males and no accessory piece.

viii. Some females have terminal papillae.

ix. The vulva is not always in the middle of the body, but may be a little anterior or posterior to it.

As a result the generic description should read:

Cuticula finely transversely striated. Worms usually appear reddish; obtuse anteriorly, more attenuated posteriorly. Mouth an elliptical dorso-ventral slit; oral cavity bounded by two lateral, pecten-shell-shaped valves united posteriorly along dorsal and ventral margins; internal walls present longitudinal posteriorly converging ridges, usually terminating at oral margin in small tooth-like spines. Valves united posteriorly at bases; a circular band-like ring is joined to valve bases covering the esophageal cap. Valves supported by two sets of dorsal and ventral prongs, usually three in each set, extending into the cuticula from valve joints. Two pairs of jaw muscles extending from the anterior valve margins to the cuticula posterior to the oral apparatus. Esophagus divided into two regions, anterior muscular, transparent; posterior opaque, probably excretory in function.

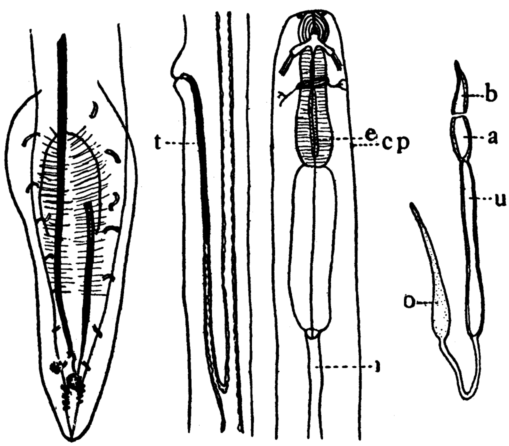
Males with recurved tails, inrolled and carrying lateral caudal alae supported by ribs. Two spicula, acuminous.

Females larger than males; tails, straight, conical, sometimes bearing minute papillae. Vulva projecting, on ventral side near middle of body; one ovary. Viviparous.

In the genus Camallanus Railliet and Henry have placed eleven species. Two others are usually considered as belonging to this group of worms but these authors do not include them in their revision of the genus. Two species have since been described by Ward and Magath (1917) and the form under consideration in the present paper adds still another.

The French authors already referred to in this paper have placed the genus in the superfamily Spiruroidea Railliet and Henry 1915 and in the family Camallanidae Railliet and Henry 1915. At present this position seems to be satisfactory.

In the past the descriptions of the members of this genus have been so brief that little information can be found in them save a few measurements; many forms will therefore have to be placed ultimately among species inquirendae. The species discussed in this paper suggests very strongly a close relationship with three others which have been previously described. One of these is a form recently discussed by Seurat (1915a) under the name *Cucullanus microcephalus* Duj. On comparing this description with that of Dujardin one is forced to say that the two forms are not the same if indeed one can identify any form from the latter's description. I therefore propose to call Seurat's material *Camallanus seurati* (Textfig. L) in honor of



Textfigure L (See page 168)

its discoverer. By a close analysis of the facts certain points of difference come out of a study of the species *C. americanus*, *C. seurati*, *C. trispinosus* and *C. microcephalus*.

II. TABLE OF COMPARISONS

Organ	*C. americanus* Magath Male	Female	*C. seurati* Magath Male	Female	*C. trispinosus* Leidy Male	Female
Mouth apparatus						
Length	0.089	0.105	0.110	0.140		
Width	0.120	0.160	0.160	0.180		
Prong length	0.080	0.105	0.110	0.140		
Number ridges	10 or 12				16	
Female tail	Three spines		Bifid		Three spines	
Female genital organs-lengths	1.3–2.1 mm.		3.1 mm.			
Ovijector	2.0–2.7 mm.		1.5 mm.			
Ovary	1.9....3.5 mm.		1.3 mm.			
Ration, ovary: oviduct	1:1.0–0.8		1:1.1			
Ova	24x25 μ		77x80 μ			
Spicula						
Right	870 μ		840 μ		450 μ	
Left	310 μ		420 μ		120 μ	
Embellishment	Single curved prong, 75 μ from from tip		Shaped like "ardillon d'hamecon," 60 μ to tip			

By reference to the descriptions one can make the following comparisons between *C. americanus* and *C. seurati*:

i. The size of the mouth apparatus is not the same in the two species. A great deal of importance should be attributed to this fact, since the structure is so constant in individuals of the same species. In *C. seurati* this structure is on the whole rather larger than in *C. americanus.*

ii. The female tail is bifid in the former species and terminates in three spines in the latter.

iii. The ovijector is longer in *C. seurati,* and the ovary and oviduct are shorter.

iv. The ova are much greater in size in *C. seurati.*

v. While the right spiculum is perhaps about the same length in the two species, the left one is not, that in *C. seurati* being a third longer. On the right spiculum there is an embellishment, which, in

the American species is, 75 μ from the tip and a simple spine in shape; in *C. seurati* the embellishment is 60 μ from the tip and in the shape of a battle axe.

There is but one item which can be compared with the new species and *C. microcephalus* as described by Dujardin. This is the size of the head, which is given by him as being 0.1 mm. in the female and 0.09 mm. in the males. While this agrees with the length of the mouth apparatus in the new species it is by no means certain that Dujardin meant to give this measurement for the length of the valves in his species. Since there are no other data which are characteristic, I regard his form as a species inquirenda.

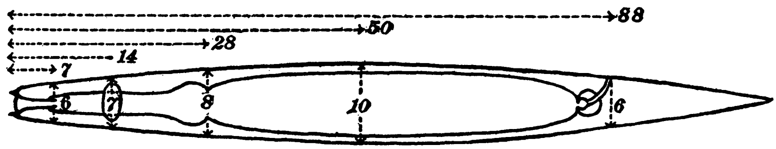
Mention should be made here that Diesing (1851) adds to the description of Dujardin's species the fact that there are three spines on the end of the female tail, but if the spines are as large as those in *C. americanus* it is hard to see how the earlier author failed to see them. It is by no means certain that Diesing had the same species that Dujardin described.

The third species is *C. trispinosus* Leidy (1851). Here again the description is so meager that one is forced to consider this as a species inquirenda for no one can identify with certainty this form from the data at hand. Leidy gave the length of the spicula as being 450 μ and 120 μ, which would be far too small for *C. americanus*, but the three spines on the end of the tail of the female is a little suggestive. He states definitely that there are eight ridges on either side of a medium on each valve, while there are only five or six in the case of *C. americanus*.

VI. NEMATODE MEASUREMENTS

Perhaps no one factor has contributed more to the chaotic condition which now exists in systematic nematode literature than the fact that authors have been content in the past to describe species by giving a few measurements and a comment or two concerning the general size and shape of some of the more prominent organs. The utter folly of describing these complex forms with a running stereotyped characterization was pointed out by Looss (1911), who stated that the trouble lay chiefly in the "way in which the new species are described." He further urged that more stress be laid upon the descriptions of parts and comparative features in nematodes.

It is not surprising that under the existing conditions some one undertook to work out a scheme for classification based upon measurements. Cobb (1890) proposed the first and only definite scheme of this kind. He devised (Textfig. M) a formula to show two kinds of



Textfigure M (See page 168)

measurements, absolute and relative, first the length of the worm and its thickness at certain points in millimeters, and secondly the percentage of that length which is represented by the distance from the anterior tip to definite points in the body. It is clear that this formula is acceptable for a species only if during the process of growth all parts increase so as to retain the original proportions, for if this is not the case then. at a given age the worms will yield a different formula than at other ages. While Cobb has used the formula for over a quarter of a century he has never attempted to defend it against the occasional criticisms of other authors, further he has never recognized that there might be some chance for unequal growth in different regions.

Fracker (1914), who confined his discussion to the parasitic nematodes, published a criticism of the formula which cast considerable reflection upon it. It is not out of place here to call attention to the fact that the table given by this author is not arranged with the animals according to size, so that, since no specific summary of the table is made, a little difficulty arises in interpreting the figures. However, he concludes that in *Oxyuris vermicularis* that "the locality of the cephalic parts of the alimentary canal tend to vary from 1 to 4 per cent., about one-third of the maximum." He also found a variation of 15% in the location of the vulva, 7% in the anus and variation in the total length and width of the body.

Looss in the work already referred to, shows quite plainly by a short table of measurements how futile it would be to try to identify *Uncinaria criniformis* or *Uncinaria polaris* on measurements alone,

and suggests in these cases that while the relative position of the genital aperture in the female is in some degree constant during individual growth, this is true in other species in the same genus, and is therefore a generic and not a specific character. All the other comparative figures vary during growth and would be of no earthly value either in the description of the species or of the genus; he has given the proportions of the length of the body to that of the esophagus, the length of the tail to the body, and the prevulvar to the postvulvar section. On the other hand he points out that the absolute length of the esophagus is fairly constant, as is also the length of the spicula and the length of the female tail, as these parts do not grow much, if at all after maturity is reached or even before. Thus he shows that in general, proportional figures are of little value, especially when they are involved in the length or thickness of the body, and that only a few organs will yield absolute measurements which can be relied upon. The points to be decided then are, which organs will yield such useful facts, how far they can be applied, and whether they are generic or specific in their compass. Such a decison will be of value because it will furnish some reliable measure or will eliminate unrealiable ones, which can never do anything more than confuse literature.

In order to test the formula system further and to see just how much weight should be placed on measurements, the author undertook a somewhat extended set of observations on individuals of *C. americanus*. For this purpose twenty females and seventeen males, picked at random from among several hundreds, have been measured and the ratios and curves worked out with a view of seeing just how much variation of parts occurs and which measurements could be relied upon. All of these worms were handled in the same manner and mounted in damar, so that the errors due to technique should be about the same in each case. Of course the number used is not very great but there can be little doubt but that, while the actual figures would be changed somewhat if more individuals had been used, the same general conclusions would be reached.*

* The tables of these measurements and the plots of curves are not published in this paper on account of the limited space. They are, however, on file in the Library of the University of Illinois, Urbana, Ill., and the Department of Zoology, University of Illinois.

(1) That an enormous variation occurs in the individuals of *Camallanus americanus* becomes evident from a study of the tables and curves. While the table includes the longest male found, the longest females are not included; the longest one ever obtained measured 30.9 mm., which if included, would give a much higher percentage of variation than is indicated in the table. Each one of the females has many embryos in the uteri, so that they must all be considered as mature females and to give a single measure for the length of the species would be extremely incorrect. The same holds true for the males altho they reach a maximum length earlier, for no embryos complicate the length factor here. Thus it appears that if the length of this species is to be given in its description, it should be accompanied with a full statement of how it was obtained, the stage to which it applies, etc., since the length variations are over 100%.

(2) While it also appears that as the worms increase in length they increase in thickness, yet one ratio will not express the relation in all individuals, since the increase in width does not parallel the increase in length; a variation of 69.4% in the females and 53.8% in the males was recorded.

(3) The size of the oral apparatus has been discussed at length elsewhere in the paper and does not appear in the table, for that region is so constant in size in both males and females that practically no difference can be detected between individuals of one sex. A ratio between the length of this structure and the length of the body or the width of each would be of no significance, since it would vary so greatly.

(4) The importance of the esophagus from a systematic and functional standpoint has been pointed out in the paper, but here it is fitting to note that this organ presents a remarkable constancy in absolute length and thickness in each sex. There seems to be no tendency for the anterior region of this organ to increase at all in length after perhaps the time of the assumption of the definitive stage, for extremely young males and females have an esophagus as long as in the older individuals, but there is some slight tendency for an increase in diameter, especially up to the time of maturity from the fourth stage. With the growth of the animals the second region of the esophagus elongates a little, not greatly and not very consistently. The data in the table shows the absolute length of the

esophagus given for any individual may vary but 11% on either side of the average, but that a ratio between it and the length of the body varies 110.5% in the females and 69.9% in males. Accordingly, in this species at least, the esophagus obtains its final length early in life and this is especilly true of the anterior region. The ratio of the first or anterior portion of the esophagus to the posterior portion varies a little more in the males than females.

(5) As the females get older and more embryos accumulate and grow in the uterus, that organ is enormously stretched and tends to fill the body cavity. As it grows the posterior horn is pushed down into the tail region; by comparison it is noted that the distance between the posterior tip of the uterus and the tip of the tail lessens as more embryos develop. This distance is, in turn, somewhat inversely proportional to the total length of the body, so that, the length of this space is, roughly speaking, an indication of the age of the worm.

(6) The length of the female tail, that is, the distance of the anus from the extreme posterior tip, is often given as a diagnostic point. In this species there is a great variation in the item. The tail grows as well as the rest of the body but not in the same proportion. Its absolute length varies 77.2% while in ratio with the length of the body a variation of 48.6% if found.

(7) As females get older the ratio between the pre- and post-vulvar region varies 50.0%, the prevulvar portion being more constant in length than the postvulvar region, this latter tending to over grow in the large individuals. It will be noted that in the young females the postvulvar region is shorter, while in the older ones this region surpasses the length of the anterior part. Without doubt the factor governing this to a great extent is the development of the embryos.

(8) It is seen that the length of the caudal alae increases with the length of the body, but that this increase is not so rapid in the caudal alae, so that a ratio between the two in no way expresses the relationship for all males, nor does the average indicate the true state of affairs.

(9) It is unfortunate that so few measurements of the spicula could be obtained, and that it is impossible to measure the length of the left spiculum in toto mounts. However, it will be seen that

very little difference in length was found in the right one, with no tendency for increase with the length of the body, the variation in length, therefore, is individual. The author has dissected out many spicula of both sides in worms varying greatly in size, and they always give a length of very nearly 870 μ and 310 μ. It therefore appears that these structures reach a full growth early in the development of these worms and do not grow later in life. A ratio between them and the body length would naturally vary considerably.

From these considerations it becomes evident that there are few if any ratios commonally given that will distinguish individuals of this species, for the range of individual variation is so great as to overlap many other species, and then too, no one set of ratios is even approximately correct or accurate for this species. The absolute length of the anterior region of the esophagus is reasonably constant, but as will be pointed out later, does not distinguish other worms of this genus. The absolute lengths, thicknesses, etc., of the mouth apparatus and the spicula are very constant and will be shown to be specific. Lengths, widths and ratios of other parts of the body are misleading and inaccurate within this species.

In connection with this work it is interesting to compare the two tables of measurements given by Breinl (1913) for a group of individuals of *Onchocerca gibsoni*. One can see from his tables that there is even more individual variation than in *C. americanus* since the esophagus and spicula vary considerably. The ratios between the parts like those taken in *C. americanus* show in the same way no close relation between the growth of the different parts, such as the length of the body and body thickness, length of the esophagus, spicular lengths, etc.

From a detailed study of the tables of measurements made from the records of previous authors and the tables already referred to of *C. americanus* the following conclusions seem justifiable:

(1) The measurements which exist are nearly as incomplete as the descriptions of the species themselves. If the facts in the case are as in *C. americanus* these measurements will not differentiate the species from one another. Even when several measurements are at hand, some species could not be differentiated from others. In the cases of *A. duodenale* and *A. conepati* there is proof for this statement. Only when the accurate descriptions of these two species are known

can they be separated, for no major differences are noted in the measurements of several of the most important organs. It is plain that two spicula might have the same length, yet one may be heavy and the other filiform, while one may be straight and the other spirally bent, conditions which would hardly justify classifying them within the same species.

(2) Tho the tables are incomplete, there seems to be a tendency for the esophagus to be fairly constant within a genus, but here and there are found exceptions. In a few cases the amount of variation found in individuals within a species has been noted, and here it can be seen that this variation will include, to a great extent, that within the genus.

(3) As in the case of the single genus Camallanus, so also with other genera, the lengths of the spicula furnish the best single characteristic. If a gubernaculum is present, its size adds additional specific information.

(4) The size of the eggs is of little or no value in the general separation of either species or genera, as the variation within a species overlaps that within a genus or even a family. Diagnosis of human parasites by observation of the eggs, e.g., in the feces, is entirely practical, for here the number of species involved is relatively small and the eggs are recognized not by the size alone, but also by their peculiar characteristics, such as the rough shell of Ascaris, the plugs at the poles in Trichuris, etc.

(5) It has been shown in the case of the species discussed in the paper, that ratios of parts and most of the absolute measurements are quite misleading in a great many respects. Cobb has used in his formula ratios and absolute lengths and thicknesses, maintaining that the value of these lay in having a number of measurements and not, as some authors give, a single item. Since it has now been shown that organs vary so greatly, a formula for one individual in a species will be as totally different from that of another as it will be from a formula of an individual in another species (Fracker 1914). In pracitcally all the cases given in the table where this variation has been indicated there is as much individual variation in a single species as there is in different species within a genus. Altho organs may increase in thickness as they do in length, the ratio is by no means

constant, and hence these ratios could not be used to designate species.

(6) It must be admitted, therefore, that the lengths and thicknesses of organs are of little value in systematic descriptions of nematodes, and if such measurements are excluded there remains only *the accurate morphological description of every organ and part of the form in question.* If this kind of information is collected there can be no doubt that it will yield results, as it has in the organization of other parasitic groups. Because of the uniformity in structure the nematodes constitute a difficult division of the animal kingdom for study, and much has yet to be done before their structures are well known as those of other parasitic divisions. Characters which are most constant in individuals should receive the greatest attention and these are usually found in the anterior and posterior regions of the body. The internal organs should of course not be overlooked, tho interest in them does not lie in measurements but in their chemical characters and morphological structure.

VII. THE CLASSIFICATION OF PARASITIC NEMATODES

In the past only one broad classification of parasitic nematodes has been offered to the attention of zoologists generally, and it was proposed by A. Schneider in 1866. He grouped the nematodes into three main divisions including certain genera under each, and omitting all other subdivisions. In free translation his classification is as follows:

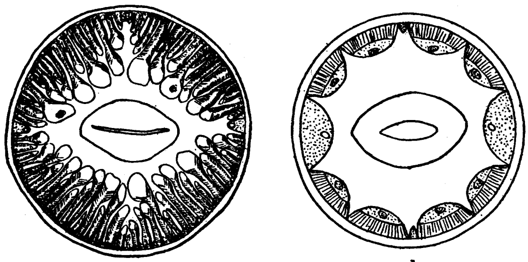
A. *Polymyarii.* Many somatic muscles are seen around the body wall in cross section. In this group are included the following genera: Ascaris, Eustrongylus, Enoplus, Physaloptera, Heterakis, Filaria, Ancyracanthus, Hedruris, Ceratospira and Cucullanus (Camallanus).

B. *Meromyarii.* Muscles of the body built up of eight longitudinal rows. Under this division are placed Nematoxys, Oxysoma, Oxyuris, Labiduris, Dermatoxys, Atractis, Spiroxis, Strongylus, Pelodera, and Leptodera.

C. *Holomyarii.* The muscles of the body not divided, or divided only by lateral bands. Anguilla, Trichina (Trichinella), Trichosoma, Pseudalius, Ichyonema, Mermis, Gordius and Sphaerularia.

Bütschli (1873) showed in the forms grouped as Holomyarii there is a separation of the ventral musculature due to the presence of the ventral nerve cord, while he and others have shown that in the other

members of the group one can find the typical longitudinal bands. As all of these members have many muscle cells in each quadrant they were placed in the first division and thus only two groups have resulted from Schneider's three (Textfig. N). However, this is not



a b

Textfigure N. Diagrammatic representation to illustrate the muscle cell arrangement described by Schneider. *a*, Polymyarii, *b*, Meromyarii. The lateral, dorsal and ventral bands are indicated.

the only objection to the system. Gordius has no place in such a classification since it is not a member of the Class Nematoda. A very heterogenous mixture resulted from the combination of the first and last groups and even in the original scheme, worms which usually have been regarded as members of the same family or superfamily are further removed from each other than from those of different superfamilies or even tribes. Thus the genera Heterakis, Ascaris and Oxyuris are separated from each other altho Mermis and Filaria are associated with Ascaris. There is no regard for any general externa feature in this classification and it is conceded by most systematists that external features are very important in the separation of groups in most cases. Further it is evident that the structure of important organs of the nematodes is not considered by Schneider. In a recent work Hall (1916) names three families under the superfamily Strongyloidea, two of which, Strongylidae and Trichostrongylidae, include Meromyarian forms while the third, Metastrongylidae, represents a Polymyarian group. He further described the superfamily Ascaroidea in which the Ascaridae and Heterakidae represent Polymyarian species while the Oxyuridae are Meromyarians. On the basis of Schneider's divisions the Oxyuridae, Strongylidae and Trichostrongylidae would be grouped together, while the Ascaridae, Heterakidae

and Metastrongylidae would belong to the group of Polymyarii. It would be absurd to think of such a grouping on the basis of present knowledge of these families. Many other objections can be pointed out and it is evident that this method of classification is not only not practical but is entirely artificial.

The following scheme for classifying nematodes was suggested by von Linstow (1897):

I. Serernentes. Along each side a lateral field with slender basis which broadens centrad and spreads out over the muscles; in one or both fields a longitudinal vessel that empties forward in an excretory pore located in the ventral line. The species live mostly in the alimentary system when sexually mature, or are free-living. The lateral fields function as kidneys. Species in the following genera are included: Ascaris, Physaloptera, Cheiracanthus, Lecanocephalus Heterakis, Cucullanus (Camallanus), Sclerostomum, Peritrachelius, Ancryacanthus, Dacnitis (Cucullanus), Spiropteaa, Spiroptenina, Leptosomatum, Oxyuris, Oxysoma, Nematoxys, Strongylus, Anchylostomum (Ancylostoma) and Trichina (Trichinella).

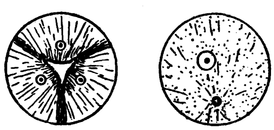
II. Resorbentes. The lateral lines are broad fields, at times one-sixth the entire circumference of the body; they have the same thickness as the muscles and carry no vessels; the excretory pore is lacking; the lateral fields appear to have an absorbtive function. The species when mature do not live in the alimentary canal of their hosts. Here are included Filaria, Filaroides, Dispharagus, Dracunculus, Eustrongylus, Ichthyonema, Pseudalius and Angiostomum.

III. Pleuromyarii. In the lateral lines stand muscles; esophageal lumen often a narrow chitinous tube, in some genera the intestine is entirely lacking. Trichosoma, Trichocephalus, (Trichuris), Gordius, Nectonema, Mermis, and Echinorhynchus.

There are several objections to this grouping. In the first place the basis of classification is purely artificial and not practical, on account of the difficulty of preparing sections to demonstrate the facts in question. The separation of Trichnella from Trichuris is of course unwarranted. The last group is a grand mixture. Gordius and the Acanthocephala are not Nematoda and have no place in such a division. Nectonema should not be considered here either. The whole system and grouping is of very little value and should not be used in the future.

In recent times certain French zoologists have been studying this group of parasites, creating many superfamilies which they divide into families, subfamilies, genera and subgenera. So far very little description of these divisions has been offered and while these investigators have brought to light many interesting and important facts, it is yet too early to accept their conclusions as final.

The last general division of the Nematoda has been made by Ward (1917), who divided them into two great divisions, the Trichosyringata and the Myosyringata. He defines the former as follows: With the esophagus of the capilliary type, consisting of "a row of cells pierced thruout the entire length by a delicate tube of minute caliber." Functionally it is evident that this type of esophagus is adapted for the passage of fluids, which must flow into the esophagus without its aid, for no musculature has been demonstrated which could assist in the process. He has termed the second group, the Myosyringata, having a pronounced muscular esophagus, with the fibers contracting transversely to the long axis of the body. "The esophagus is tripartite in cross section" and functions for the taking in of food by opening up a lumen lined with cuticula and triangular in cross section when open. This causes a powerful suction and draws in fluids or solid food. This grouping included in the Myosyringata all the families of the nematodes save the Trichotrachelidae and the Mermithidae, which are placed in the Trichosyringata (Textfig. O).



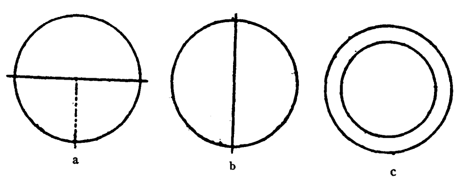
Textfigure O. Diagrammatic representation illustrating the basis of Ward's nematode divisions. *a*, Myosyringata type of esophagus in cross section. *b*, Trichosyringata type of esophagus in cross section.

Many authors have suggested in the morphological descriptions of nematodes the importance of the esophagus and it has been stated that as a class, the Nematoda have a tripartite muscular esophagus shaped like a club. This statement is not entirely true for there are several forms known in which the esophagus is not of this character

but as has been mentioned before, is of the capilliary tube type. As yet there is no very good explanation as to how these two types have arisen, but some very suggestive facts have been learned which at a later date may help to clear up the matter. However this be, it is certainly true that for purposes of classification these two types are easily distinguished and furnish a natural and logical division of the class. The author has pointed out some of the important features of the esophagus and it is very fitting that this structure should be selected as the primary basis for the separation of the nematode orders. For the subsequent division of these groups a great deal of investigation will be necessary, yet at the present time some suggestions are not out of place.

Since the smaller group contains forms of such varied nature there will be no difficulty in finding characters which will differentiate groups among them. For example, there are forms in which the males have but one spicule, while others have two, some in which the males have but one testis. Again there are forms which have bacillary bands, etc. These are more or less radical departures from the usual types and careful study will, without doubt, separate out groups very easily. Since the Myosyringata contain the majority of nematodes and these are more nearly alike each other than the Trichosyringata, the subdivisions here will be harder to make, all the more so when the morphological data are so scanty.

Several possibilities have presented themselves, one of which seems to be particularly fundamental, and uses the oral apparatus for the separation of groups. It has been shown that at least three distinct conditions exist which are as follows (Textfig. P.):



Textfigure P. Diagrammatic representation of the three fundamental types of oral parts which have been demonstrated for certain nematodes belonging to the Mysosyringata. *a*, the dorsalventral type, *b*, the lateral type, and *c*, the circular or true buccal capsule type.

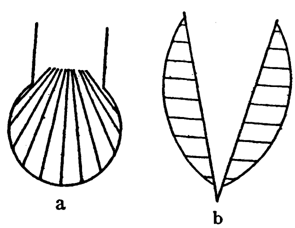
1. A mouth built up, on the dorso-ventral plan. An example of this is found in Ascaris, where there are three lips, but so placed that one is dorsal and two ventral and that the division between the lips for the mouth opening extends from right to left.

2. Lateral mouth parts, of which the genus Camallanus furnishes an interesting case. Here the whole structure is devised on the lateral plan, there being two lateral lips or jaws, with the mouth as a dorso-ventral slit. It is obvious that the two types are radically different and can be readily distinguished.

3. In the last type the mouth is arranged on the circular plan. Here there is a true buccal capsule which is perhaps best understood in the hookworms. The mouth parts of Camallanus are therefore fundamentally different from those of the group to which the hookworms belong and from a functional standpoint the mouth parts of the former are really jaws.

Physiologically there seems to be some difference between these three types. The first are munchers, the second grasping forms and the last suckers. Other groups based on different conditions of the oral parts will be found when more species are carefully studied.

A great deal of confusion has resulted from the loose usage of the terms "bursa," "alae" and "wings." The caudal end of the male is often modified so that there exists an expansion of cuticula enclosing the whole posterior end. This is supported by cuticular tubes filled with muscles, which radiate outwards like the spread out fingers of the hand (Textfig. Q). For this structure the term bursa



Textfigure Q. Diagrammatic representation to show the difference between a "bursa" and "wings" at the posterior end of certain male nematodes. Note that in *a*, the bursa is supported by *rays* which arise from a common locus, while in *b*, the wings are supported by *ribs* which have separate origins.

should be used. In other forms the cuticula is split laterally forming narrow wings, which are supported by small ribs of cuticula, or the wings may meet medially on the ventral side, the median wall of each wing breaking down and leaving the space open all the way across. However in either case the supporting structures arise from separate places along the body wall. These forms should be stated to possess wings or alae. Still other male nematodes have no modification of the posterior cuticula save the presence of papillae, while some may not even have these. Thus at least four subdivisions are possible on the basis of differences in the male tail. It is also important to note that corresponding differences are to be noted in the morphology of the vulva of the females which must be accomodated to the characteristics of the male tail of that species.

Not only does the esophagus furnish a good organ upon which to base the first separation of groups, but it also furnishes possibilities for further subdivision. Ward and Magath (1917) have pointed out some of the possibilities and at present at least four distinct types are known. The first of these consists of the simple muscular esophagus without any modifications; in the second type the esophagus has a bulbous enlargement on its posterior end; in the third type one finds ceca attached to the posterior end and these may be associated with ceca from the intestine. Several different varieties may be distinguished according to whether the ceca point anteriorly, posteriorly etc. The fourth type of esophagus modification occurs in those cases in which one finds regional differentiations in the esophagus, which may take the form of granular portions, septal divisions, etc. Other types probably exist but lack of information of a morphological character necessitates this point being left open.

Generic and specific classification will not be such a great task once the larger divisions are made, because one deals in the nematodes with so many different organs and variations of these organs. It is not the author's intention to point out these items at the present time, but the careful study of the exact morphological details of many species of nematodes will result in as firm a basis of classification of this group of animals as exists in any other group.

VIII. SUMMARY AND CONCLUSIONS

1. The material used for this study was *Camallanus americanus* nov. spec., found in the small intestine of turtles of the following species and in different parts of the United States of America: *Chlydra serpentina, Chrysemys marginata, picta, scripta, trossti* and *elegans, Malacoclemmys lesuerri* and *Aromochelys odoratus.* The percentage of infection is nearly eighty and most turtles yield about fifteen to twenty parasites. They have not been found in the few soft-shelled turtles examined.

2. The description of the genus Camallanus Railliet and Henry 1915 is corrected and amended according to new facts learned.

3. *Camallanus americanus* is distinguished from the most closely related species by the size of the hard parts and their shape, by conditions in the female reproductive system and by the female tail. These are the only points that can be compared since these are all that are given by previous authors. A nematode called by Seurat "*C. microcephalus*" has been shown to be a new species and is named *Camallanus seurati.*

4. Evidence is given to demonstrate the inadequacy of nematode ratios as distinguishing features. Some absolute lengths seem to be specific, others tend to embrace the whole genus. Descriptions of nematodes based on a few measurements and ratios of organs are valueless. Measurements are secondary to the careful description of the parts of the worms and only in the case of the hard parts can one place any confidence in absolute lengths or thicknesses. Cobb's nematode formula is fallacious, at least as regards the parasitic species. The esophagus obtains a maximum length early in life, but later grows somewhat in thickness. The members of the genus Camallanus are poorly described and many cannot be identified from the descriptions given since they contain only a few measurements and little of fundamental morphological description.

5. The morphology of every system of *Camallanus americanus* has been studied and given in detail.

(a) The cuticula is uninteresting morphologically but from a chemical standpoint presents a number of important problems. It has been shown that the cuticula is not chitin but cornein, an albuminoid probably related to the supportive tissue proteins of other animals.

(b) The structure of the subcuticula and the longitudinal lines has been given in detail; the "filling in" tissue of the anterior end is not a ligament as Looss supposed, but represents the anterior mass of the subcuticula, which supports the nervous structure of the anterior end and perhaps forms the oral apparatus. Here there is cell constancy.

(c) The function of excretion is undoubtedly divided between the lateral lines, canals and the posterior portion of the esophagus. There is a single bridge cell which is in contact with the accessory tissue around the esophagus.

(d) The somatic musculature is of the type designated by Schneider as Polymyarii, but is on the dividing line between the types called Platymyaria and Coelomyaria. Part of the somatic muscles of the ventral half of the caudal end of the male are modified for helping in the act of copulation. They pull up the ventrum of the body thus drawing together the two caudal alae, which in turn grip the projecting vulva of the female.

(e) The intestinal muscle cells are described for the male and female, and the musculus ani for the female. Their mechanisms are given.

(f) The mouth apparatus is built on the lateral plan. It is opened by two pairs of muscles, large and modified from the somatic muscle cells.

(g) The esophagus is divided into two portions; the anterior muscular and the posterior granular and probably excretory. Cell-constancy perhaps exists. The dorsal esophageal gland has a single nucleus and the excretory tissue of the esophagus has two very large nuclei. There is an esophageal gland.

(h) The intestine is typical and has in it a great deal of pigment. There is little doubt but that this pigment is the result of some stage in the metabolism of blood of the host.

(i) Details of the rectum and the cloaca are given. Looss' position taken as regards the rectal cells and his so-called "rectal ligament" is not accepted.

6. The chief food of this species is the blood of the host.

7. The red color of the worms is due to the color of the body fluid; it is without doubt some product from the host's blood. Tissue acting like mesenteries to hold the organs in place is present.

8. The reproductive system of the female is interesting. Only the anterior ovary and oviduct are developed and the latter contains a seminal recepticle. The species is viviparous and the uteri of the adults are filled with embryos. Some of these are already contained within their first skin which is shed a short time after birth.

9. Two unequal, acuminous spicula exist in the males and the typical nematode male reproductive organs are present. The spermatozoa in the seminal recepticle are oriented with their long axes parallel to the long axis of the oviduct. Circular muscles are around the ductus ejaculatorius and this region probably secretes a carrying fluid for the spermatozoa.

10. The nervous system is simple and like most nematodes, consists of a nerve ring, anterior ganglia, longitudinal nerves and posterior ganglia. The anal ganglion is simple and in the male there are large posterior lateral ganglia which supply the anal papillae or ribs. These ganglia are most likely homologous with the three pairs of posterior lateral ganglia in Ancylostoma.

11. The innervation of the two lateral cervical papillae and the alar ribs of the male have been studied and the details of the nervous endings given. Both are connected to the exterior by special structures.

12. A few young females have been found in the several examinations made for these parasites. They are probably in the fourth stage, and differ from the adults in three essential respects, viz., the condition of the cuticula, the oral apparatus and the genital organs. In them the vulva is not indicated and the opening to the exterior is not yet effected.

13. The importance of the species is pointed out and the members of the superfamily Spiruroidea are given a place between the free-living forms and the Trichosyringata, on the one hand, and the higher forms such as the ascarids on the other. They are therefore very important and are mostly parasites of water hosts.

14. Possibilities for the future classification of the Nematoda are shown and Ward's fundamental divisions, the Trichosyringata and Myosyringata, are accepted. His secondary division, based on the condition of the oral parts is deemed logical and natural.

15. Nematode classification cannot hope to make a great advance, however, until more species are accurately and minutely described.

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LIST OF ABBREVIATIONS

ac t	accesso excretory around the esophagus
a g	anal ganglion
a-g o	ano-genital opening
al	caudal alae
an	anus
ant e	anterior portion of the esophagus
ant u	anterior uterine branch
a sv c	anterior subventral nerve cell
b c	excretory bridge cell
c c	carrying cell of the excretory duct
c g	cloacal ganglion
cl	cloaca
c p	cervical papilla
c t	cone tissue, posterior portion of the esophagus
de	ductus ejaculatorius
d l	dorsal line
d n o	origin of the dorsal nerve
e d	excretory duct
e g	dorsal esophageal gland
e g n	dorsal esophageal gland nucleus
e m	extensor muscle of the spiculum
e n	posterior portion of the esophageal excretory tissue nucleus
e v	esophageal valve
f	nucleus of the ovum
fb	fibrillar portion of muscle cell
f i m	fibrous tube enclosing the intestinal muscles
g	genital fundement
g m	giant muscle cell of the oral valve
i	intestine
i dk	inner dark layer
i l	inner light layer
i m	intestinal muscle
i m n	intestinal muscle nucleus
i sph	intestinal sphincter
l c	lateral commissure
l c g	lateral cephalic ganglion
l e c	lateral excretory canal
l g	lumbar ganglion
l l	lateral line
l n	lateral nerve
l sp	left spiculum
l v	lateral valve of the oral apparatus
m	ordinary muscle cells of the esophagus
m a	musculus ani
m a n	musculus ani, nucleus
m c	somatic muscle cell
m l	muscular layer of the ovijector
m m	marginal muscle of the esophagus
m n	nucleus from the spermatozoon
n r	nerve ring
n r c	nerve ring cells
nz	nutritional zone
o	ovum
ob m	oblique muscles of the tail of the male
od	oviduct
o dk	outer dark layer
o l	outer light layer
ov	ovary
ovj	ovijector
p-a p	para-anal papilla
p b	polar body
pj	projections from the lining of the seminal recepticle
po-a p	post-anal papilla
post e	posterior portion of the esophagus
post u	posterior uterine branch
pr-a p	pre-anal papilla
p v c g	post ventral cervical ganglion
p v l	projections from the somatic muscle cells to the ventral line
rach	rachis
rec	rectum
rec c	rectal cells

rec l	rectal lining
r es	esophageal cap or the ring of the oral apparatus
r g	rectal ganglion
r m	retractor muscles
r sp	right spiculum
sb t	subcuticular tissue, "filling-in tissue"
sc	sarcoplasmic portion of a somatic muscle cell
s e	esophageal sphincter
s i l	spindle cells lining the ovijector
sp	spiculum
sp c	spicular canal
sperm	spermatozoa
sph	sphincter
s r	seminal receptacle
sr g	sub-rectal gland
s v	seminal vesicle
td	trident
tr	trompe
u	uterus
v	vestibule
v c	valve cover of the oral appartus
v c g	ventral cervical ganglion
v c g c	ventral cervical ganglion cell
v l	ventral line
vul	vulva
v v	vulva valve
w	anterior wing of the oral apparatus
x	shedding skin of the first stage
z	juncture of the anterior and posterior portions of the esophagus

EXPLANATION OF FIGURES

PLATE VII*

Fig. 1. Lateral view of the oral apparatus of a male.

Fig. 2. Dorsal view of the oral apparatus of a female.

Fig. 3. Anterior end of a male, lateral view.

Fig. 4. Anterior end of a young female, lateral view.

Fig. 5. Vulva of an adult female, lateral view. The uterus is filled with living embryos.

Fig. 6. Posterior end of an adult male. Only the right spiculum is shown.

Fig. 7. Posterior end of a young female, immature. Lateral view.

Fig. 8. Posterior end of an adult female. Lateral view.

Fig. 9. Vulval region of an immature female.

Fig. 10. Larva of the first stage in the uterus of the female. Note the four anterior nuclei.

Fig. 11. Head of a larva beginning the fourth stage. Drawn from life, note the four anterior nuclei. The reference line is 10 μ long.

PLATE VIII†

Fig. 12. Transverse section thru the anterior portion of the oral apparatus.

Fig. 13. Transverse section thru the middle of the oral apparatus, section in series with figure 12.

Fig. 14. Transverse section thru the ring of the oral apparatus and in series with figures 12 and 13.

Fig. 15. Transverse section thru the anterior tip of the oral apparatus of an immature female.

Fig. 16. Transverse section thru the middle of the oral apparatus of an immature female and in series with figure 15.

Fig. 17. Detail of the angle of the oral valves of an adult.

Fig. 18. The trident, drawn trom a dissection, medial view.

Fig. 19. Detail of the angle of the oral valves of an immature female.

Fig. 20. The valve cover, drawn from a dissection.

Fig. 21. A spindle cell from the lining of the ovijector.

Fig. 22. The anterior wings of the oral apparatus, drawn from a dissection, slightly displaced.

Fig. 23. The anterior wings of the oral apparatus, drawn from a dissection.

Fig. 24. The ring of the oral apparatus, drawn from a dissection.

Fig. 25. Structure of a somatic muscle cell from the anterior half of the body, transverse section.

Fig. 26. Longitudinal section of the cuticula of an adult.

Fig. 27. Transverse section of the cuticula of an adult.

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* Each line on this plate represents a length of *40* μ, except in Figure 11.

† Each line on this plate represents a length of *10*μ.

Fig. 28. Structure of a somatic muscle cell from the posterior half of the body, transverse section.

Fig. 29. Outline of a longitudinal section of the cuticula, to show the striations.

Fig. 30. Transverse section of the anterior portion of the esophagus.

Fig. 31. Transverse section of the posterior portion of the esophagus.

Fig. 32. Longitudinal section thru the cuticula of an immature female.

Fig. 33. Transverse section of the posterior portion of the esophagus, thru the excretory tissue nuclei.

PLATE IX*

Fig. 34. Sagittal section thru the anterior portion of the body.

Fig. 35. Frontal section thru the anterior portion of the body.

Fig. 36. Transverse section thru the esophageal valve.

Fig. 37. The two excretory nuclei and gland cell nucleus of the esophagus.

Fig. 38. Longitudinal section thru the lower end of the esophagus and upper end of the intestine.

Fig. 39. Transverse section thru the anterior cone of tissue in the posterior portion of the esophagus.

Fig. 40. Longitudinal section thru the juncture of the anterior and posterior portions of the esophagus.

Figs. 41–45. Transverse sections of the lining of the anterior portion of the esophagus, in order passing posteriadly. Figure 41 is at the extreme anterior end and figure 45 at the extreme posterior end.

PLATE X†

Figs. 46–55. Series of transverse sections from the same worm, beginning with the first section just at the anterior level of the esophagus. The last figure in the series is figure 51, which is thru the bridge cell. The figures are arranged in sequence on the plate but not in regard to the numbering.

Fig. 56. Transverse section thru the bridge cell of an immature female.

Fig. 57. Transverse section thru lateral line and lateral excretory canal.

PLATE XI‡

Fig. 58. Transverse section thru the vulval valve.

Fig. 59. Longitudinal section thru the ovijector.

Fig. 60. Transverse section thru the vulva.

Fig. 61. Transverse section thru the ovijector near the uterus.

Fig. 62. Transverse section thru the ovijector sphincter at the point where it turns outward.

Fig. 63. Sagittal section thru the vulva.

Fig. 64. Longitudinal section thru the juncture of the oviduct with the uterus

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* Each line on this plate represents a length of *10 μ*, except in Figure 38 where it is *40 μ* long.

† Each line on this plate represents a length of *20 μ*.

‡ Each line on this plate represents a length of *10 μ*, except in Figures 65, 66, 67 where it is *100 μ* long.

Fig. 65. Outline of the beginning of the ovijector and the uterus.

Fig. 66. Outline of the anterior portion of the reproductive organs of a female.

Fig. 67. Outline of the posterior ending of the female reproductive organs.

Fig. 68. Fertilization of the ovum.

Fig. 69. Transverse section of the anterior region of the ovijector of an immature female; the beginning of the sphincter.

Fig. 70. Middle region of the ovijector of an immature female, in transverse section.

Fig. 71. An uterine wall cell.

Fig. 72. Transverse section of the ovijector; middle region.

Fig. 73. Transverse section of the zone of "growth."

Fig. 74. Transverse section of the germ zone.

PLATE XII*

Fig. 75. Longitudinal section thru the seminal recepticle.

Fig. 76. Oblique section thru the oviduct.

Fig. 77. Oblique section below the anus of a male.

Fig. 78. Transverse section thru the seminal recepticle.

Fig. 79. Transverse section thru the ano-genital opening of a male.

Fig. 80. Transverse section thru the middle of the body of a male.

Fig. 81. Transverse section thru the ductus ejaculatorius.

Fig. 82. Spermatozoa.

Fig. 83. Transverse section of the anterior region of the testis.

Fig. 84. Sagittal section thru the posterior region of the body of a male.

Fig. 85. Transverse section of the reproductive organ in an immature female.

Fig. 86. Transverse section at the insertion of the retractor muscle on the head of the right spiculum.

Fig. 87. Transverse section thru the posterior portion of the body of a male.

Fig. 88. Transverse section thru the right spiculum, below the head.

Fig. 89. Transverse section thru the left spiculum below the head.

Fig. 90. Transverse section thru the head of the right spiculum.

Fig. 91. Detail of the external end of a preanal papilla.

Fig. 92. Sagittal section thru the posterior portion of the body of a male and thru the juncture of the digestive and reproductive tracts.

PLATE XIII†

Fig. 93. Distal end of the right spiculum, from a dissection.

Fig. 94. The right spiculum, from a dissection.

Fig. 95. The left spiculum, from a dissection.

Fig. 96. The right spiculum within its sheath, from a dissection.

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* Each line on this plate represents a length of *10* μ, except in Figures 84, 87 and 92 where it is *20* μ long.

† The lines for Figures 93-101 represent a length of *20* μ, those for Figs. 102–112, a length of *10* μ.

Fig. 97. Transverse section thru the posterior region of a male, above the region of the caudal alae.

Fig. 98. Sagittal section thru the posterior region of a male.

Fig. 99. Oblique frontal section thru the posterior region of a male.

Fig. 100. Oblique frontal section thru the posterior region of a male and passing thru the spicular canal.

Fig. 101. Outline of the anterior ending of the testis.

Fig. 102. Detail of the cephalic papilla to show the entrance of the nerve. The section is longitudinal.

Fig. 103. Longitudinal section thru the right spiculum, proximal end.

Fig. 104. Transverse section of the seminal vesicle.

Fig. 105. Longitudinal section thru the retractor muscle of the spiculum to show the type of nucleus.

Figs. 106–109. Details of the nerve cells from the lateral cephalic ganglion.

Fig. 110. Detail of the lateral cephalic papilla, showing the chromatin ending of the nerve and the "trigger."

Fig. 111. Longitudinal section thru the posterior portion of the lateral cephalic ganglion and the cervical papilla.

Fig. 112. The juncture of the seminal vesicle and the ductus ejaculatorius; longitudinal section.

PLATE XIV*

Fig. 113. Sagittal section thru the posterior portion of the body of a female, passing thru the anus.

Fig. 114. Sagittal section of the posterior region of the body of a female and passing thru the middle of the rectum.

Fig. 115. Transverse section thru the intestine of a mature female.

Fig. 116. Sagittal section thru the posterior region of the body of a female, and passing thru the anus. Almost a median section.

Fig. 117. Transverse section in the post-anal region of a female.

Fig. 118. Transverse section thru the posterior third of the body of a female.

Fig. 119. Transverse section thru the musculus ani of a female.

Fig. 120. Transverse section of the same worm as figured in figure 118 and somewhat posterior to the latter figure.

Figs. 121–122. Transverse sections thru larvae of the last part of the first phase, in the uterus of the female.

Fig. 123. Transverse section posterior to figure 120, and from the same worm.

Fig. 124. Transverse section thru the ovijector of an immature female.

Figs. 125–128. Transverse sections in series thru the rectal sphincter region.

Fig. 129. Transverse section thru the nucleus of the intestinal muscles of a female.

Figs. 130–131. Two sections in series passing thru the rectum of the same female as figure 118.

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* Each line on this plate represents a length of *10 μ*, except in Figures 113, 114, 116, where it is *40 μ* long.

PLATE XV

Fig. 132. Longitudinal section thru the oral apparatus of *C. americanus*, showing the mode of attachment in the intestine of the turtle. Photomicrograph.

Fig. 133. Transverse section thru the oral apparatus of *C. americanus*, showing the mode of attachment to the intestine of the turtle. Photomicrograph.

Textfigure F. Illustrating Perrier's principle of the action of the lateral valves of Camallanus. After Perrier (1872).

PLATE XVI

Figure 134. Redrawn from Seurat. *C. seurati*; *a*, distal region of the anterior uterine branch; *b*, terminal region of the posterior uterine branch; *e*, excretory pore; *i*, intestine; *o*, ovary; *p*, postcervical papilla; *t*, "trompe"; *u*, region of the uterus which is occupied by the eggs.

Textfigure O. Cobb's nematode formula (Redrawn from Cobb), 6, 7, 8, 10, 6 are the transverse measurements, while 7, 14, 28, 50, 88 are the corresponding longitudinal measurements. The formula in this case is:—

$$\frac{7. \quad 14. \quad 28. \quad 50. \quad 88.}{6. \quad 7. \quad 8. \quad 10. \quad 6.}$$

The unite of measurement is the hundredth part of the length of the worm, whatever that may be. The measurements become, therefore, percentages of the length. The measurements are taken with the animal viewed in profile; the first is taken at the base of the pharynx, the second at the nerve-ring, the third at the cardiac constriction, the fourth at the vulva in females and at the middle (*M*) in males, the fifth at the anus.

Most of the drawings were made by Mr. C. W. Shepard of the Department of Anatomy, College of Medicine, University of Illinois.

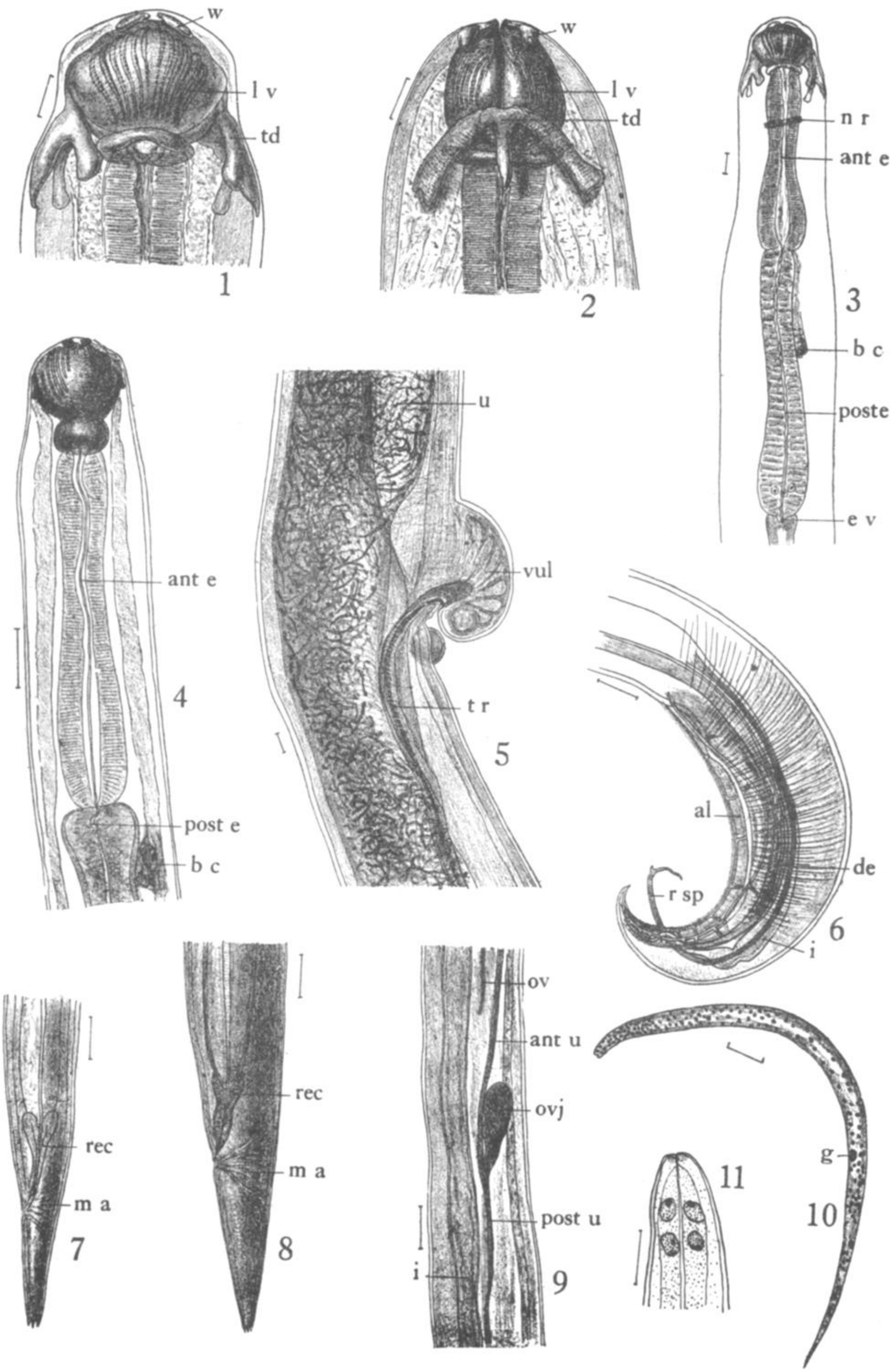

PLATE VII **MAGATH**

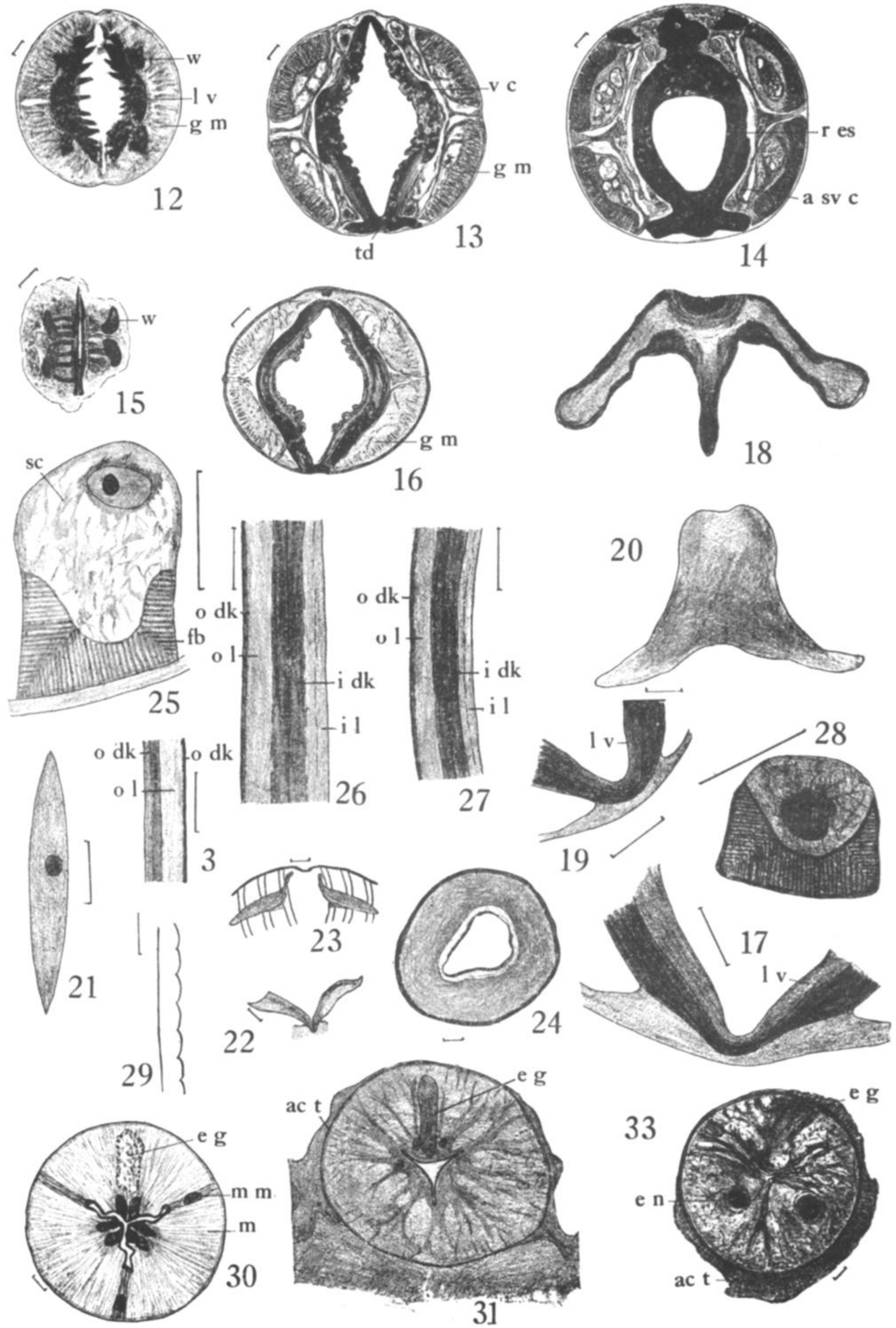
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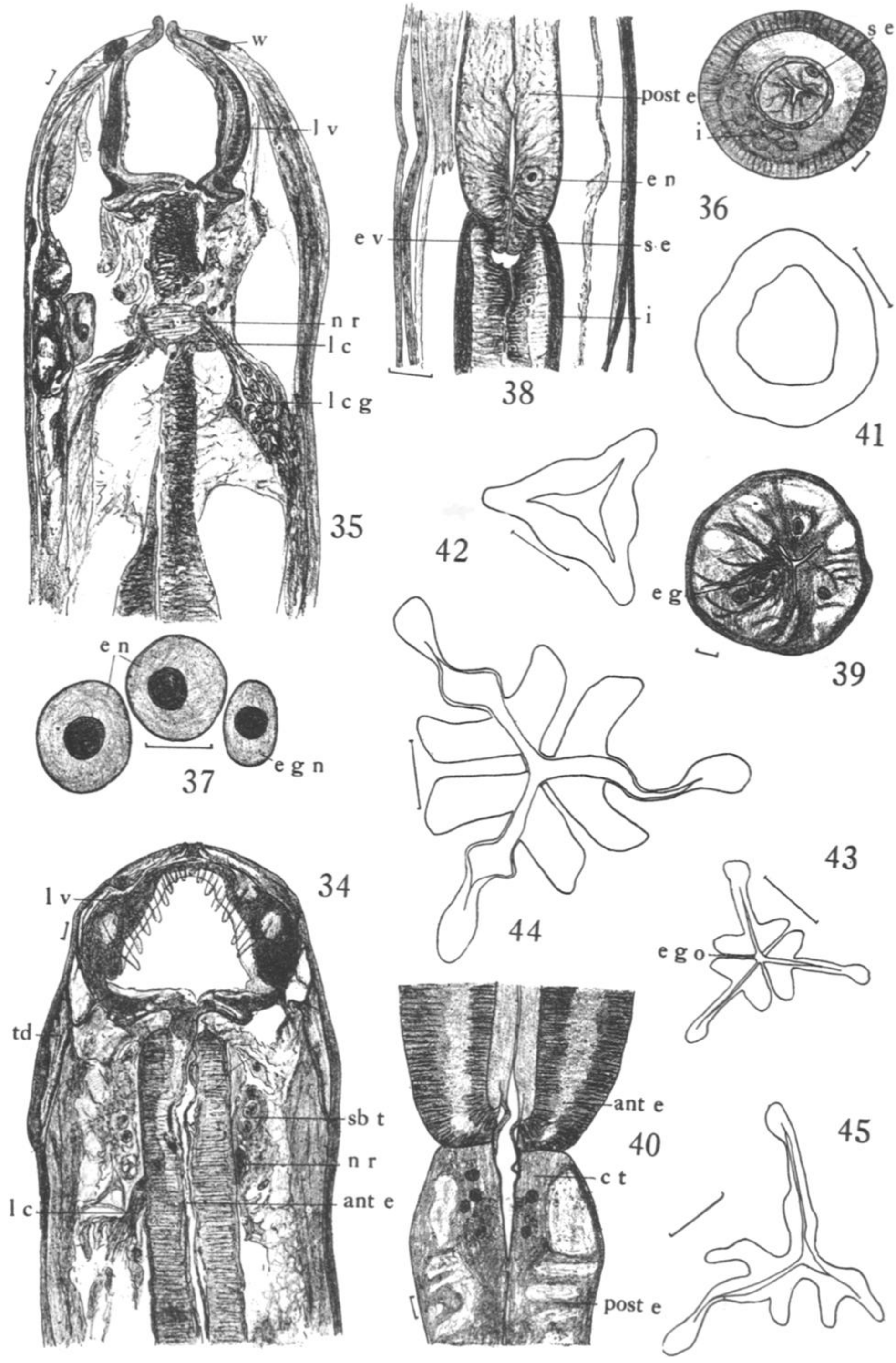
PLATE VIII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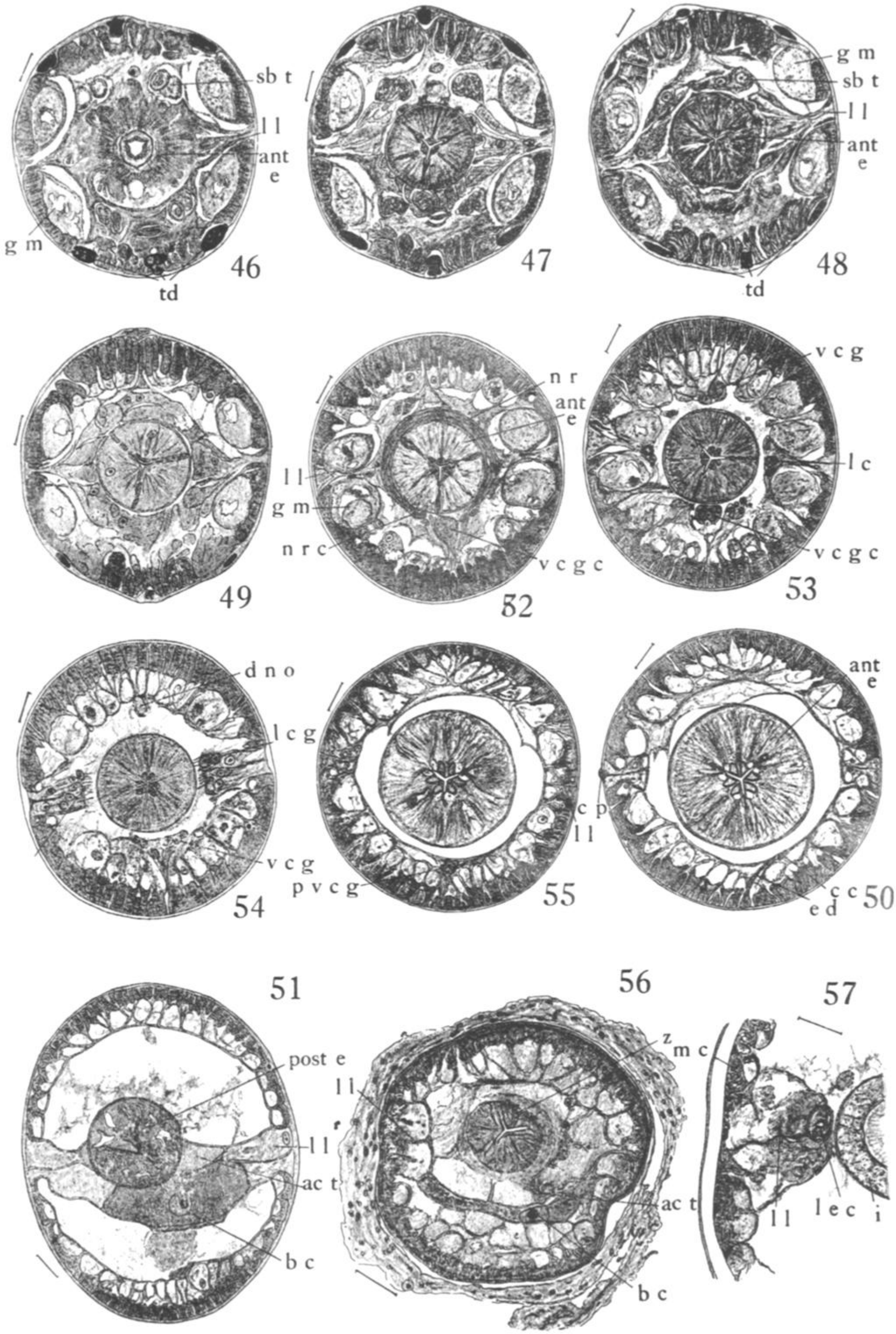
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PLATE X

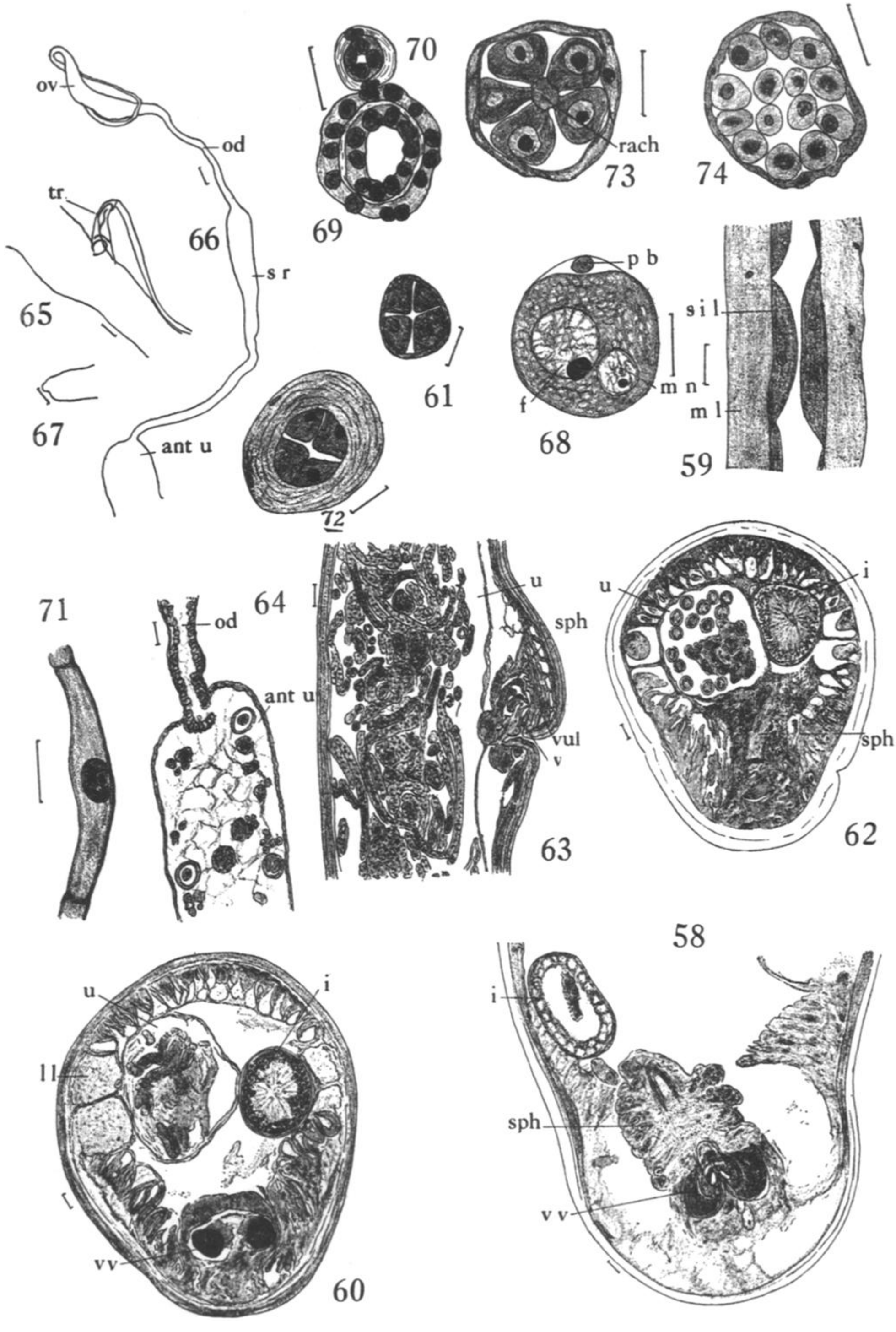

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PLATE XI

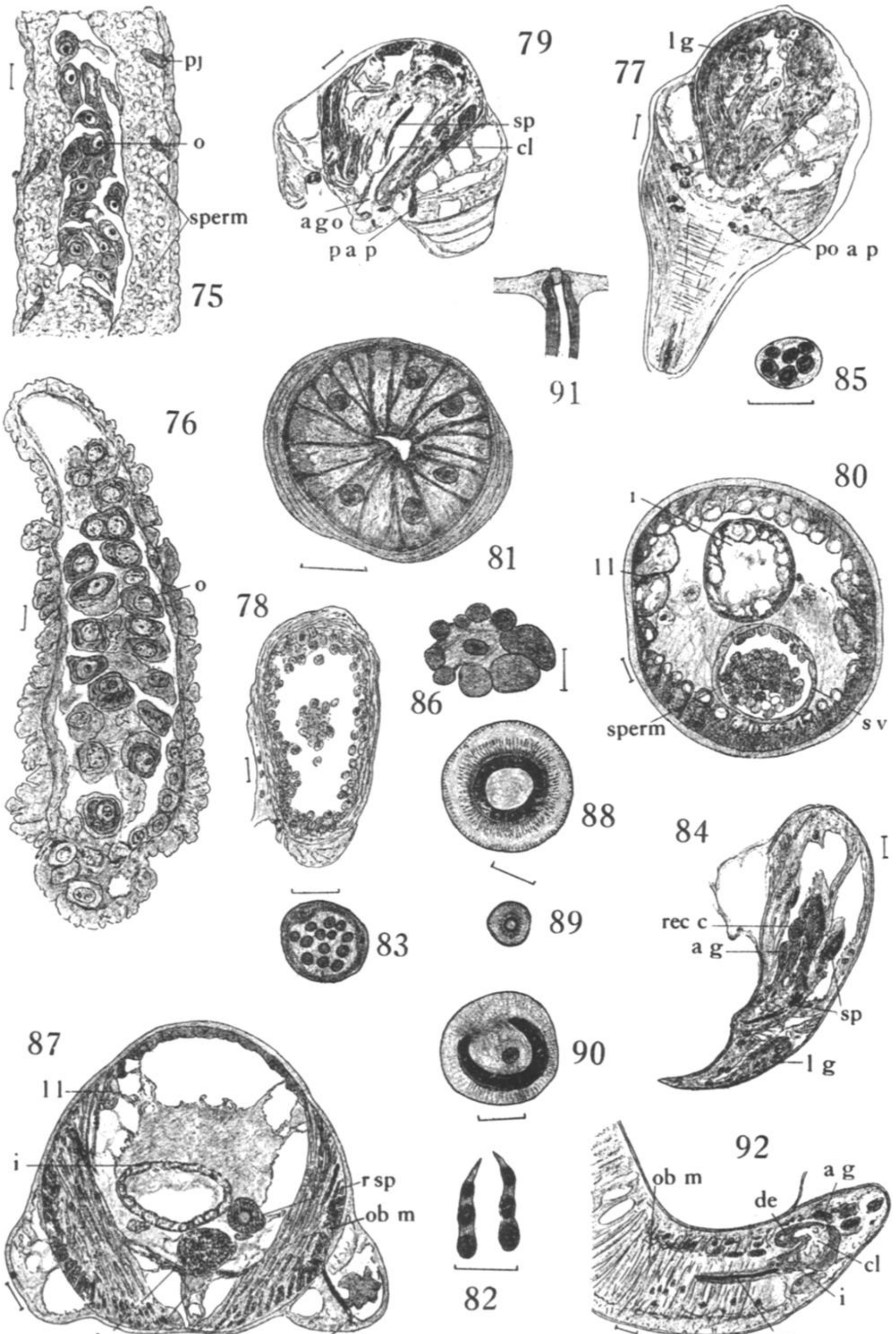

PLATE XII **MAGATH**

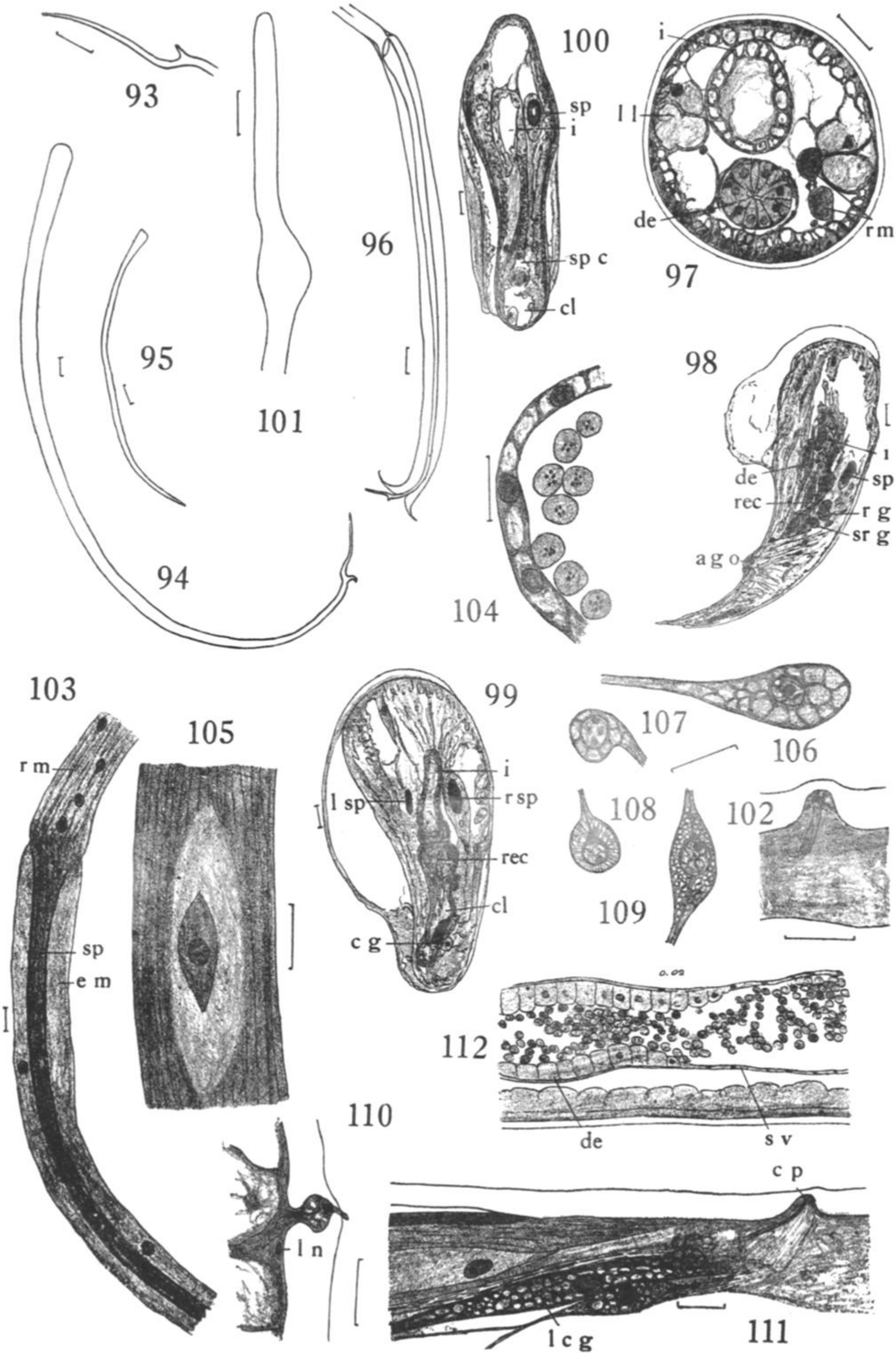
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PLATE XIII

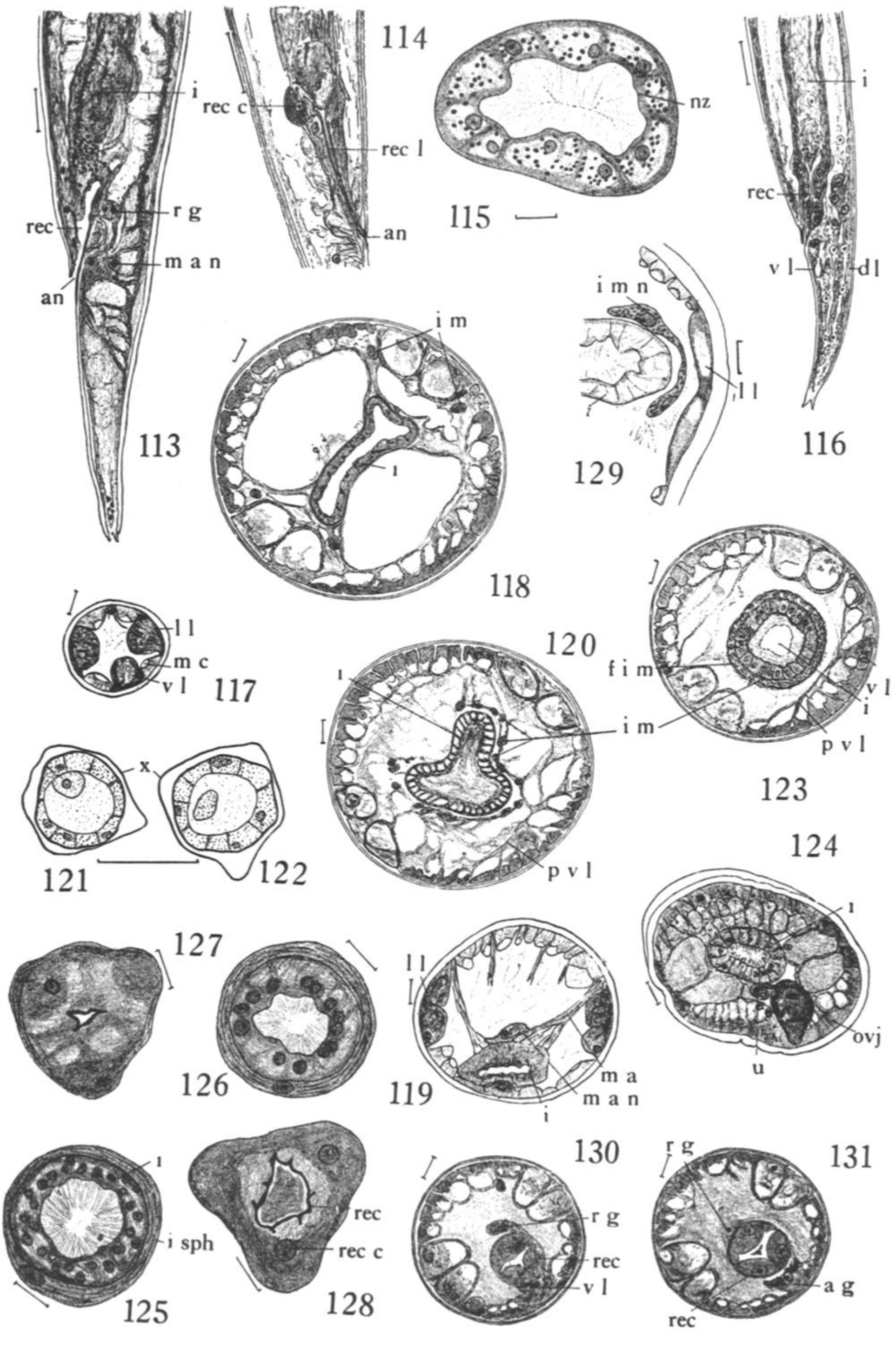

PLATE XIV

MAGATH

PLATE XV MAGATH